JOURNAL OF AGRICULTURAL RESEARCH

VOL. XXI WASHINGTON, D. C., JUNE 15, 1921 NO. 6

BIOLOGY AND ECONOMIC IMPORTANCE OF ANASTATUS SEMIFLAVIDUS, A RECENTLY DESCRIBED EGG PARASITE OF HEMILEUCA OLIVIAE

By D. J. CAFFREY

Scientific Assistant, Cereal and Forage Insect Investigations, Bureau of Entomology, United States Department of Agriculture

INTRODUCTION [1]

Adults of the recently described egg parasite *Anastatus semiflavidus* Gahan were first reared from eggs of the New Mexico range caterpillar, *Hemileuca oliviae* Ckll., during the progress of experiments to determine methods for the economic control of that destructive pest.

These rearings were made by F. H. Gates from *Hemileuca oliviae* eggs collected in the vicinity of Koehler, N. Mex., during June, 1913. For several years prior to this date extensive egg collections in the same vicinity and throughout the infested area had failed to reveal the presence of any egg parasite of *H. oliviae*.[2] It is assumed from the foregoing that, just before the period during which these negative collections were made, some severe and unusual climatic condition had reduced the numbers of the parasite to such an extent that its presence was not discovered at that time. Since its discovery in 1913 the parasite has appeared in increasing numbers each year until it now exerts a powerful influence in the natural control of its host.

DISTRIBUTION OF THE PARASITE

Egg collections made during the autumn of 1915 and the winter and spring of 1916 demonstrated that the parasite was widely distributed in that part of northeastern New Mexico which was heavily infested by the range caterpillar. Adults were reared from the following localities in that section: Maxwell, Brackett, Nolan, Las Vegas, Springer, Chico, Cimarron, Mora, Watrous, Miami, Colfax, Folsom, Wagon Mound, Vermejo, Koehler, Colmor, Taylor, Levy, Roy, Mills, and Clayton.

[1] The observations detailed in this paper were made principally at the United States Range Caterpillar Camp near Koehler, N. Mex., and at the United States Entomological Laboratory, Maxwell, N. Mex. V. L. Wildermuth, F. H. Gates, W. F. Schlupp, and H. E. Smith assisted in securing the data herein presented.

[2] AINSLIE, C. N. THE NEW MEXICO RANGE CATERPILLAR (HEMILEUCA OLIVIAE CKLL.). *In* U. S. Dept. Agr. Bur. Ent. Bul. 85, pt. 5, p. 59-96, fig. 32-53, pl. 3-4. 1910.

CLASSIFICATION AND DESCRIPTION

Anastatus semiflavidus belongs to the hymenopterous superfamily Chalcidoidea, family Encyrtidae, and subfamily Eupelminae. It was described as a new species by A. B. Gahan,[1] of the Bureau of Entomology, from type specimens reared from *Hemileuca oliviae* eggs by F. H. Gates at Koehler, N. Mex. Mr. Gahan's description of the adult follows.

ADULT

Anastatus semiflavidus, new species. *Female* [Pl. 68, A].—Length, 2.3 to 2.5 mm. Head strongly punctate; eyes elliptical; antennal pedicel about two-thirds the length of the first funicle joint; ring-joint transverse; first, second, and third funicle joints subequal, following joints shorter; mesoscutum with the median and lateral lobes alike faintly scaly-punctate and hairy; the median lobes more distinctly sculptured bordering the lateral margins; scutellum and axillae very finely and closely punctured, the former precipitous posteriorly and the posterior face smooth; propodeum smooth; mesopleurae mostly smooth, but with the anterior portion above scaly-punctate; postmarginal vein twice as long as the stigmal, the marginal a little more than twice the postmarginal; abdomen faintly lineolate, about as long as the thorax. Scape reddish-yellow, flagellum black; head brassy-green; mesoscutum, punctate area on the mesopleurae, posterior face of the scutellum, propodeum, hind coxae, and underside of the thorax metallic blue-green; scutellum and axillae varying from wholly pale orange-yellow to dark brown, with only the bases yellowish; remainder of the thorax reddish yellow; legs yellowish within and along the margins, blackish or brownish outwardly, the femora often tinged with metallic; wings fuscous, the base hyaline to the beginning of the marginal vein and a broad hyaline transverse band before the stigmal vein; abdomen yellowish above except the three apical segments, which are darker and somewhat metallic; venter pale at base, brownish medially and metallic apically.

Male [Pl. 68, B].—Head strongly punctate; antennal scape compressed and expanded beneath, pedicel very short, flagellum tapering slightly from base to apex; first funicle joint about twice as long as wide; following joints successively shortening; club scarcely as long as the two last funicle joints combined; mesoscutum and scutellum alike scaly-punctate, mesopleurae mostly smooth; propodeum smooth; postmarginal vein nearly as long as the marginal and a little more than twice the length of the stigmal; abdomen reticulately lineolate. Color dark blue-green; antennae black, the expansion of scape pale; abdomen beyond the first segment brownish-black; all trochanters, a line above and the apices of front and middle femorae, front tibiae outwardly for its whole length, basal third of middle and hind tibiae and the three basal joints of the middle and hind tarsi yellowish white; front tarsi and apical two joints of the other tarsi fuscous; remainder of the legs blue-green or blackish.

Type-locality.—Koehler, New Mexico.

Host.—*Hemileuca oliviae.*

Type.—Cat. No. 18331, U. S. N. M.

LARVA

The freshly dissected larva (fig. 1) is dirty white in color with the body contents showing darker. When viewed dorsally, the general shape is elliptical, becoming slightly broader posteriorly. When viewed later-

[1] GAHAN, A. B. DESCRIPTIONS OF NEW GENERA AND SPECIES, WITH NOTES ON PARASITIC HYMENOPTERA. *In* Proc. U. S. Nat. Mus., v. 48, p. 155-168. 1914.

ally, the larva appears crescent-shaped and is slightly depressed dorso-ventrally. The head is partly retracted and not chitinized. The mandibles are small and almost invisible. The body segments, 13 in number, are well defined and slightly broader dorsally than ventrally. This causes a well-defined fold just above the pleural areas which becomes more pronounced posteriorly. A narrow ridge extends down the median line dorsally. The head and first two body segments are sparsely pubescent.

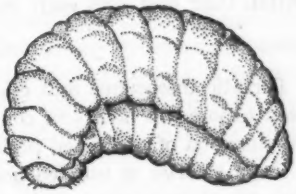


FIG. 1.—*Anastatus semiflavidus:* Larva, side view. Greatly enlarged.

The average dimensions of the larva are: Length when extended, 2.5 mm.; width, 1.25 mm.; depth dorso-ventrally, 1 mm.

PUPA

The pupa (fig. 2) when first formed is creamy white in color and closely resembles the adult in shape. The appendages are folded close to the body, and the entire pupa is covered by a thin pupal skin. The sex differences are early apparent. The female pupa, when extended, averages 2.5 mm. in length, and the male pupa, 1.75 mm. Soon after formation, the eyes of both sexes turn pink and gradually the thorax and abdominal bands of the female become light brown in color, while in the male they become dark blue-green. Just before the emergence of the adult, the entire pupa assumes the characteristic color of its sex.

FIG. 2.—*Anastatus semiflavidus:* Pupa, side view of female. Greatly enlarged.

LIFE HISTORY

EGG PERIOD

All attempts to dissect the egg of *Anastatus semiflavidus* from its host or to ascertain the length of the incubation period have been unsuccessful.

The period of normal oviposition in the field begins when the *Hemileuca oliviae* eggs are first deposited, about the middle of September, and continues until the arrival of severe winter weather, which occurs in these comparatively high altitudes during late November or early December.

Judging from indications furnished by numerous dissections of host eggs from life-history cages and from eggs collected at various times in the field, it is probable that the parasite eggs which are deposited just before the beginning of cold weather hibernate in that stage, while the eggs which are deposited early in the season hatch and hibernate as

partly developed larvæ within their host. This theory would account for the presence of the fully developed larvæ that are frequently found within their host eggs early in the succeeding spring.

LARVAL PERIOD

Periodic dissections and emergence records of egg clusters that had been exposed to adults in confinement indicated extreme variations in the duration of the larval period for different individuals.

From a series of isolated host egg clusters that had been exposed to parasite adults in cages for two days during the last week of September, 1914, a few adults emerged early in May, 1915. The larval period of these individuals therefore was limited to about seven months, whereas some of the other eggs in these same egg clusters were found to contain full-grown dormant larvæ nearly two years later—that is to say, in March, 1917.

Dissections of 1- and 2-year-old eggs collected in the field gave similar results and established the fact that on some occasions the insect remains in a dormant larval state for at least two years.

It will be apparent from the foregoing that any statement concerning the duration of the larval period must necessarily be in approximate terms.

PUPAL PERIOD

The pupal period is evidently very short, as in a long series of dissections of parasitized eggs, made at intervals of three or four days, it was observed that pupæ were rarely found, although many of these eggs contained fully developed larvæ and adults were emerging each day.

Pupæ were dissected out of the host and placed in different types of cages in an attempt to ascertain the length of the pupal period, but none were reared through to the adult form.

ADULT PERIOD

In laboratory experiments the females remained alive for several weeks in Doten cages that were supplied with equal parts of honey and water as food. Under these same conditions the males remained alive but a few days after being placed in the cages.

Adults have been observed in the field from the early part of May until the first of December, the maximum emergence occurring during July and August. As the host eggs are not deposited until September, it is probable that the females live for long periods under field conditions, the length of their life depending upon the proximity of their host and upon the weather conditions.

DURATION OF LIFE CYCLE

From a series of 49 cages started in September and October, 1914, a total of 383 adults were reared. These adults required a maximum of

449 days and a minimum of 226 days to complete their life cycle, the average being 380 days. (See Tables I and II for a record of two of these cages.) From a series of cages started in October, 1915, a total of 40 adults were reared. These adults required a maximum of 346 days and a minimum of 238 days to complete their life cycle, the average being 266 days. From a series of stock cages started the last week in September, 1914, adults were reared from the first week in the following May until March, 1917, a minimum of 7 months and a maximum of 30 months. It is evident that this prolonged life cycle was not due to the artificial cage conditions because adults emerged from 1- and 2-year-old eggs collected in the field.

TABLE I.—*Duration of life cycle, proportion of sexes, and progeny of one female Anastatus semiflavidus*

Cage No.	Date egg was exposed.	Date adult parasite emerged.	Total number of days.	Number and sex of adults.	Result of dissecting eggs still intact on May 20, 1916.
	1914.	1915.			
817 (1)	Sept. 17	Sept. 22	370	2 ♂, 1 ♀	
		26	374	1 ♀	One living larva.
		30	378	1 ♀	Two dead larvæ.
		Oct. 26	404	2 ♀	
		Dec. 4	443	1 ♀	
817 (2)	18	Sept. 22	369	1 ♂, 2 ♀	One living larva.
817 (3)	20	Oct. 22	397	1 ♀	Do.
		Dec. 10	446	1 ♀	One dead female.
817 (4)	22	Sept. 3	344	1 ♂	
		22	365	2 ♂	One living larva.
		24	367	2 ♀	
817 (5)	25	24	364	1 ♀	
		25	365	1 ♀	Do.
		Oct. 19	390	1 ♀	One dead larva.
		Nov. 16	418	1 ♀	Do.
		20	422	1 ♀	
817 (6)	27	May 17	233	1 ♂	
		Sept. 22	360	3 ♀	
		25	363	2 ♀	
		26	364	1 ♀	One living larva.
		30	369	1 ♀	
		Oct. 2	371	1 ♀	
		4	373	1 ♀	
817 (7)	29	Sept. 22	358	2 ♂	
		24	360	1 ♂	
		26	362	2 ♀	One dead larva.
		30	366	2 ♀	
		Oct. 25	392	1 ♀	
817 (8)	Oct. 1	Sept. 7	342	1 ♂	

Average number of days in life cycle= 373.4.
Maximum number of days in life cycle= 446.
Minimum number of days in life cycle= 233.
Proportion of sexes= 12 males and 32 females.
Total progeny of one female= 54 individuals.

Many experiments were carried on to determine whether this parasite would reproduce in mature eggs. No reproduction was secured in any of these experiments.

The extreme variation in the duration of the life cycle, as shown in Tables I and II, is important in that it would allow the parasite to survive any unfavorable weather conditions for an extended period.

TABLE II.—*Duration of life cycle, proportion of sexes, and progeny of one female Anastatus semiflavidus*

Cage No.	Date egg was exposed.	Date adult parasite emerged.	Total number of days.	Number and sex of adults.	Result of dissecting eggs still intact on May 20, 1916.
	1914.	1915.			
818 (1)	Sept. 18	July 24	309	1 ♂	Three dead larvæ.
		Aug. 1	316	1 ♂	
		24	339	1 ♂	
		Dec. 7	445	1 ♂	
818 (2)	20	Sept. 22	367	2 ♀	
		24	369	1 ♀	
		27	372	1 ♀	
		30	375	1 ♀	
		Oct. 8	383	1 ♀	
818 (3)	22	.....	.....	.....	No parasitism.
818 (4)	25	Sept. 22	362	1 ♂	One dead larva.
		24	364	1 ♂, 2 ♀	One dead male.
		Dec. 9	440	1 ♂	
818 (5)	27	Sept. 24	362	2 ♀	
		Oct. 17	385	1 ♀	One dead female.
		26	394	1 ♀	
818 (6)	29	Sept. 22	358	1 ♂, 1 ♀	
		24	360	1 ♀	
		25	361	1 ♂, 1 ♀	One living larva.
		26	362	1 ♀	
		Oct. 10	376	1 ♂	
		22	388	1 ♂	
818 (7)	Oct. 1	Sept. 30	364	1 ♂, 1 ♀	
		Oct. 8	372	1 ♀	
		12	376	1 ♂	One dead larva.
		21	385	2 ♂, 1 ♀	
		Nov. 7	402	1 ♂	
818 (8)	3	May 17	226	1 ♂	Four dead larvæ.
		Sept. 3	335	1 ♀	One dead pupa.
		22	354	3 ♀	Two dead females.
		25	357	1 ♀	
		Nov. 7	400	1 ♂	
818 (9)	5	Sept. 28	358	1 ♀	
		Oct. 25	385	1 ♂	

Average number of days in life cycle= 366.7.
Maximum number of days in life cycle= 445.
Minimum number of days in life cycle= 226.
Proportion of sexes= 20 males and 29 females.
Total progeny of one female= 60 individuals.

CAGE REARING METHODS

The cages used in experiments with *Anastatus semiflavidus* adults were of a modified Doten type.[1] This cage consisted of two round 30 by 100 mm. glass vials, of the same diameter and shape, cut off squarely at the open ends. A small patch of beeswax was melted on the inside of one vial, at a point equidistant from each end, to serve as a support for the food of the Hymenoptera. This food consisted of equal parts of honey and water and was applied as a small drop in a depression made in the beeswax. This vial was known as the food tube. The other vial was known as the home tube and was left in its original condition.

The Hymenoptera were introduced into the home tube, and the open ends of the two vials were placed together. A strip of heavy wrapping paper, 2 inches wide and 10 inches long, was then bandaged tightly around the abutting edges and secured by snapping a heavy rubber band around each vial at the edge of the paper bandage.

When it became necessary to change the food tube for replenishment or cleaning, a duplicate food tube was prepared to replace the original. Before this change could be affected, however, it was necessary to entice the Hymenoptera into the other, or home tube. This was accomplished by holding the home tube with its closed end toward the light and inclined slightly upward. A smart tap on the bottom of the food tube would usually drive any insects into the home tube that refused to crawl out. When all the Hymenoptera in the cage had moved into the home tube, the rubber band holding the original food tube was removed. The other rubber band on the home tube held the paper bandage in position while the newly prepared food tube was quickly inserted and its rubber band replaced.

In life-history experiments it became necessary to introduce egg clusters of the host into these cages. Under these circumstances, the Hymenoptera were enticed into the food tube, after which the home tube was removed, the host egg cluster quickly inserted, and the home tube returned to its original position.

The glass sides of this cage made it possible to follow easily the activities of the insects under observation, and its mobility allowed it to be placed upon the binocular stage for microscopic examination of its contents.

The labels and other necessary data were written on the paper bandage holding the two vials together.

The cage was prevented from rolling and smearing the honey solution over the interior by placing it in a shallow pasteboard box with loose cotton.

[1] DOTEN, Samuel B. CONCERNING THE RELATION OF FOOD TO REPRODUCTIVE ACTIVITY AND LONGEVITY IN CERTAIN HYMENOPTEROUS PARASITES. First paper. Nev. Agr. Exp. Sta. Tech. Bul. 78, p. 8-10, pl. 1. 1911.

Adults of *Anastatus semiflavidus* were kept alive for long periods in this type of cage, provided proper care was exercised in its maintenance. The honey solution was kept fresh, a new supply being prepared every few days, as experience demonstrated that a rancid or moldy condition of the food caused the death of the Hymenoptera. The interior of the cage was kept strictly clean and free from all particles of dirt or other foreign matter that would entangle the insects.

The direct rays of the sun proved fatal to the confined insects, so it was necessary to keep the cages in a shaded location.

HABITS

FERTILIZATION

The union of the sexes and the fertilization of the female take place in the manner common to most chalcids soon after the adults emerge and last but a few seconds.

When this species was first reared from *Hemileuca oliviae* eggs, it was thought that the male and female *Anastatus semiflavidus* were separate species. Each sex was accordingly exposed to eggs of *H. oliviae* in separate cages for the purpose of securing life-history records. Under these conditions, the species proved parthenogenetic, as all the progeny of the unmated female *A. semiflavidus* were males.

OVIPOSITION

The process of oviposition was often observed in life-history cages. In one instance, a female of *Anastatus semiflavidus* was introduced into a glass vial cage containing a *Hemileuca oliviae* egg cluster known to have been deposited 2 days previously. This female had been confined in a stock cage containing many adults of both sexes and had probably been fertilized. It had not previously been exposed to any eggs of its host. Immediately upon being introduced into the cage, the female began examining the egg cluster, running over the surface of the eggs and feeling them with her antennæ. After 2 or 3 minutes she apparently selected an egg that suited her purpose and began making preparations to oviposit. V. L. Wildermuth then took this female under observation and through the binocular microscope observed the details of the process of oviposition. He states that in the two instances under his observation the female drilled a hole in the shell of the egg with her ovipositor in 15 and 20 minutes, respectively, after which an egg was apparently deposited in each instance. Mr. Wildermuth then directed the writer to observe the details of oviposition and to describe the same. After a short interval this cage was again examined by the writer, and soon the female was observed making preparations to oviposit.

Through the binocular microscope, it was seen that the female was poised over the selected egg, the legs being strongly braced against the sides of the adjoining eggs, and most of the pressure being exerted

through the posterior pair of legs. The ovipositor protruded a short distance (fig. 3), and the abdomen moved slowly up and down, forcing the ovipositor into the shell of the egg. Occasionally the movement was from side to side, and there were short intervals of rest.

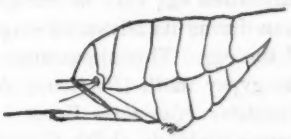


FIG. 3.—*Anastatus semiflavidus:* Side view of posterior segments of female abdomen with extruded ovipositor. Greatly enlarged.

After 21 minutes, the opening in the egg appeared to be completed and a small drop of brownish liquid appeared at the point where the ovipositor was inserted in the egg. It is impossible to state whether this liquid exuded from the female or came from the egg. When this operation of drilling an opening in the egg was complete, the female turned around and examined the puncture. She appeared to be sipping the liquid around the opening in the eggshell or possibly feeding on the contents of the egg. The female soon resumed her original position and inserted the ovipositor into the egg, nearly full length. The ovipositor was then partly withdrawn and thrust again into the egg. This operation was repeated 9 or 10 times. Finally the ovipositor was thrust in full length, the female crouched low over the egg, the abdomen, meanwhile, was drawn sharply forward, and oviposition apparently took place. The female remained quiet, except for a slight movement of the abdomen, in this act of oviposition for 2 or 3 minutes. The ovipositor was then withdrawn, and the female turned around and manipulated the mandibles and antennæ in the small drop of liquid which remained over the opening in the egg. This liquid soon hardened and formed a transparent, light brown, waxy substance which apparently sealed the oviposition puncture. After completing oviposition in this egg, the female resumed her examination of the remaining eggs in the cluster and was observed to oviposit several times during the remainder of the day.

INTERNAL APPEARANCE OF PARASITIZED EGG

For a long period after oviposition the internal appearance of a parasitized egg does not differ from the normal, the contents consisting of a reddish brown liquid. The only change apparent, until the parasite larva becomes visible, is a slight thickening of the liquid contents. In the course of its development, the larva consumes these liquid contents and finally occupies about two-thirds of the egg-cavity. Only one larva develops in each egg.

EXTERNAL APPEARANCE OF PARASITIZED EGG

Superficially the external appearance of a parasitized egg does not differ from the normal, there being no change in its color or shape. Microscopic

examination, however, reveals the presence of the sealed oviposition puncture, and this is the only external indication by which a parasitized egg may be recognized. The parasite can not be discerned, even during its advanced stages, through the opaque, thick-walled shell of the egg. This appearance is in marked contrast to that of eggs of the gypsy moth (*Porthetria dispar* L.) which have been parasitized by *Anastatus bifasciatus* Fonsc. The parasite larva of this closely allied species is plainly visible through the shell of its host egg.

Hemileuca oliviae larvæ frequently hatch from eggs bearing oviposition punctures of the parasite. This is probably due to the fact that these particular eggs were not successfully parasitized.

APPEARANCE OF HOST EGGS FROM WHICH ADULTS HAVE EMERGED

The adult, upon emerging from the pupa, finds itself completely inclosed within the walls of the host egg. It gnaws a small but easily distinguishable hole through this wall and makes its escape.

The host eggs from which *Anastatus semiflavidus* adults have issued may be readily recognized by the presence of this exit hole. It is much smaller than the hole made by the hatching of the host larvæ. (Pl. 68, C.)

METHOD OF LARVAL DEVELOPMENT

The larva of *Anastatus semiflavidus* prevents the formation of the embryonic larva of its host and feeds exclusively upon the liquid contents of the host egg. This method of larval development is characteristic of the true egg parasites.

DORMANT PERIOD OF FULL-GROWN LARVA

After the larva has become full-grown, the development of the pupal stage depends largely upon the external climatic conditions to which the egg is subjected. In northern New Mexico, these climatic conditions refer especially to humidity and must be considered in this special sense. The degree of humidity as affecting the development of parasite larvæ in this semiarid climate depends largely upon whether the eggs are situated on high or low ground, or upon the distance from areas of surface water.

If the parasitized egg, containing a full-grown larva, happens to be subjected to a long period of drought, pupation may be delayed and a dormant larval period of indefinite duration produced until such a time as both humidity and temperature are favorable for further development.

When these favorable conditions occur, the full-grown dormant larva changes to a pupa without regard to the length of time spent in the larval stage.

SHORT LENGTH OF PUPAL PERIOD

The duration of the pupal period is very short, as noted by numerous dissections. From this fact it is assumed that the insect must be less

resistant to adverse weather conditions as a pupa than as a dormant larva or as an adult, and it would appear that the pupal period is made as short as possible in order to hurry the insect through the most vulnerable period of its existence. The few pupæ dissected from parasitized eggs have invariably been found during periods of heavy adult emergence.

NUMBER OF INDIVIDUALS PRODUCED BY EACH FEMALE

In cage experiments, two females under observation produced 60 and 54 individuals, respectively (Tables I and II). These figures may be considered as being below the average, because under natural conditions each female probably produces a greater number of progeny than when confined in cages.

JUMPING HABIT OF ADULTS

Although equipped with wings, the adults of both sexes appear to lack the power of sustained flight. Locomotion seems to be accomplished largely by means of jumping or running. Adults that were observed in the field running around on the ground in the vicinity of host egg clusters disappeared with startling rapidity when an attempt was made to collect them, their movements, when approached, resembling those of the halticine flea-beetles. This ability to jump made the species very difficult to handle in the laboratory cages, and many adults were lost during the process of feeding or when they were being transferred from one cage to another.

The males are much more active than the females.

RELATIVE PROPORTION OF SEXES

From a quantity of *Hemileuca oliviae* eggs collected in the field a total of 393 adults issued. Of this number 158 were males and 235 were females. From two series of life-history cages a total of 423 adults issued. Of this number 175 were males and 248 were females. These figures would seem to indicate that both sexes were well represented but that the females were slightly more abundant than the males. (Tables I and II.)

POSITIVELY PHOTOTROPIC HABIT OF ADULTS

The adults of *Anastatus semiflavidus* are positively phototropic. This characteristic was used to advantage in rearing the adults from eggs collected in the field and in handling the species in life-history cages.

HOSTS OTHER THAN HEMILEUCA OLIVIAE

Adults of *Anastatus semiflavidus* were reared from eggs of *Hemileuca nevadensis* Stretch, collected from willow along the banks of the Red River in New Mexico. Laboratory experiments also demonstrated that

adults of *A. semiflavidus*, emerging from *H. oliviae* eggs, would breed in eggs of *H. nevadensis*.

The eggs of this closely allied species are not very numerous in the region infested by *Hemileuca oliviae* and, therefore, do not form a very important host for *Anastatus semiflavidus*. If for any reason, however, *H. oliviae* should become greatly reduced in numbers, the eggs of *H. nevadensis* would serve as a valuable host in perpetuating *A. semiflavidus*. From many indications, it is probable that such a condition of affairs has existed in the past. A study of the life history of *H. nevadensis* demonstrated that its life cycle and that of *H. oliviae* correlate very closely.

An attempt was made to rear *Anastatus semiflavidus* from the eggs of *Malacosoma fragilis* Stretch, collected from scrub oak along the foothills, and to secure parasitism of these eggs in confinement, but only negative results were obtained.

ECONOMIC IMPORTANCE OF THE PARASITE

It has been very noticeable that this highly beneficial insect has been increasing rapidly in numbers since the spring of 1913 when the species was first discovered. This increase has been especially marked in areas of heavy *Hemileuca oliviae* infestation.

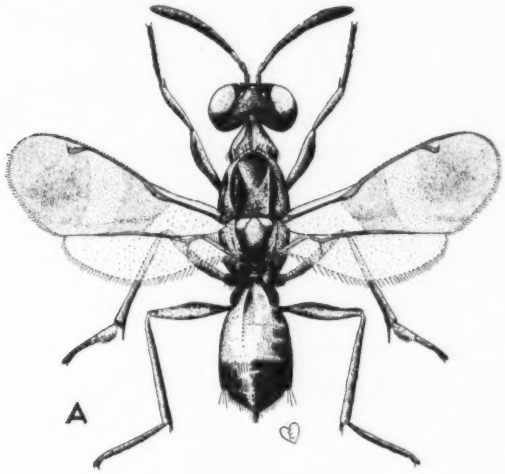
In the collections of *Hemileuca oliviae* eggs made from different localities during the autumn of 1915 and the winter and spring of 1916 the percentage of parasitism varied from 75 to only a trace. The species was found to be present in every locality from which *H. oliviae* eggs were collected with the exception of two isolated areas far to the south of the main area of infestation, in which only a very few egg clusters were found.

At the present time *Anastatus semiflavidus* appears to be one of the most efficient natural enemies contributing to the control of *Hemileuca oliviae*.

PLATE 68

Anastatus semiflavidus:

A.—Adult female, dorsal view.
B.—Adult male, dorsal view.
C.—Exit holes of adults from egg clusters of *Hemileuca oliviae.*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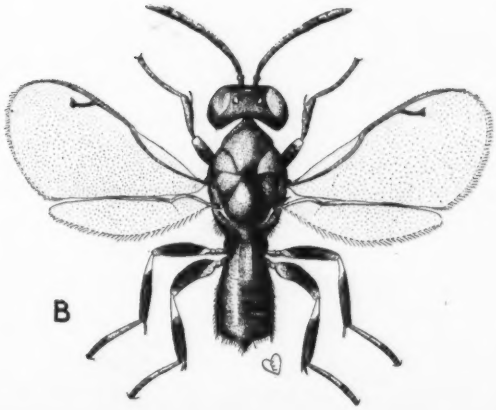
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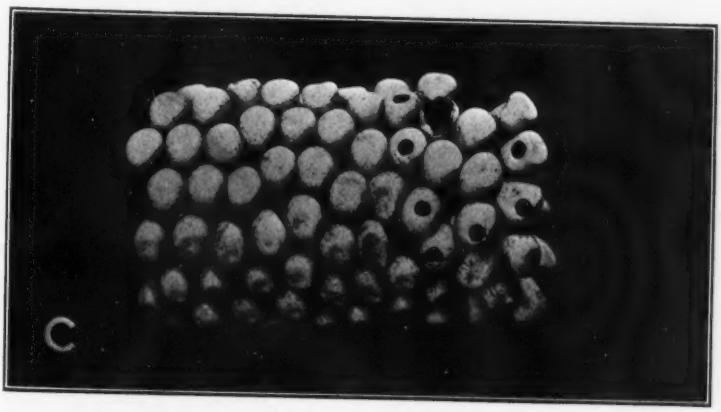
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VARIETAL SUSCEPTIBILITY OF BEANS TO RUST [1]

By F. D. FROMME, *Plant Pathologist*, and S. A. WINGARD, *Assistant Plant Pathologist*, *Virginia Agricultural Experiment Station*

INTRODUCTION

The bean rust fungus, *Uromyces appendiculatus* (Pers.) Fries, is worldwide in distribution, being found practically coextensive with the distribution of its hosts throughout the North American continent and in the West Indies, South America, Europe, Africa, Asia, Japan, and Australia. In addition to its common host, *Phaseolus vulgaris* L., it occurs in North America on ten species of Phaseolus, two species of Dolichos, two of Strophostyles, and three of Vigna (*1*).[2] It is an autoecious species with the full complement of spore forms. The aecia are of the cupulate type and are of rather rare occurrence, judging from the collections in herbaria. The writers have seen them in the field on only one occasion. The uredinia and telia are found during the summer and fall and are very common. The relative importance of the different spore forms in the overwintering of the rust has not been determined, but it seems likely that the teliospores are of minor importance, at least under Virginia conditions, and that the urediniospores are the most important factor in overwintering.

In the opinion of the writers bean rust is commonly underrated as a limiting factor in bean production. The losses are indirect, being occasioned by decreased vigor due to foliage injury, and this fact tends to obscure the amount of curtailment of yield except in very severe cases. Although the disease occurs in all parts of the United States losses seem to be especially severe in Virginia, West Virginia, Tennessee, and southern Ohio of the eastern States, in Georgia and Louisiana of the southern States, and in California. In the commercial bean areas of the North it seemingly appears too late as a rule to cause much injury. It is occasionally severe in the New England States. In Virginia bean rust is one of the chief limiting factors in production. Severe injury is commonly found on three varieties, Kentucky Wonder, Navy Pea, and Tennessee Green Pod. Evidence of the severity of bean rust in California and of the inefficacy of spraying may be seen in the following quotations. R. E. Smith (*10*) in discussing the work at the California Experiment Station says:

> Mr. Rogers did a considerable amount of work during the year in an endeavor to find means for checking a serious rust (*Uromyces appendiculatus*) which attacks the

[1] Published with the approval of the Director of the Virginia Agricultural Experiment Station. Paper 56 from the Department of Plant Pathology and Bacteriology.

[2] Reference is made by number (italic) to "Literature cited," p. 404.

Journal of Agricultural Research, Washington, D. C.
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Vol. XXI, No. 6
June 15, 1921
Key No. Va. (Blacksburg)-3

Kentucky Wonder bean in San Diego county and prevents the growing of this valuable crop late in the fall. Treatment both with Bordeaux mixture and finely ground sulfur was tried, but unfortunately neither material gave any appreciable control of the disease.

D. C. Milbrath [1] is quoted as follows:

In Los Angeles county, especially in the San Gabriel Valley, rust developed so rapidly on beans during the past week that some fields have been abandoned. This is the case particularly with Lady Washington and French varieties.

Until recently there has been little specific information in literature on the relative susceptibility of bean varieties to rust.

Duggar (*2*) states that great differences exist in the susceptibility of varieties among both dwarf and pole sorts and suggests that the selection of resistant varieties would seem to be possible.

Gassner (*5*) noted a difference in the susceptibility of 2 varieties of beans in South America and later planted 15 varieties in a field test. These were inoculated with rust spores, and wide variations in susceptibility were seen. Three of the varieties were severely injured, while the remainder were only moderately, slightly, or not at all affected.

Jordi (*7*), in Europe, took field records on five varieties of pole beans with respect to severity of rust, using the cipher 1–10 to indicate the state of susceptibility. Four of the varieties were susceptible, being rated 7–10, while one, Klosterfrauen, was resistant, being rated only 0.5–1.

In the Plant Disease Bulletin for September 15, 1918, W. J. Morse (*9*) lists 17 varieties of beans with respect to their susceptibility to rust in Maine. Seven of the varieties were severely attacked, while the other 10 developed only slight infection or none.

In a previous publication (*4*) the writers have described the field behavior of a large number of bean varieties with respect to their susceptibility to rust. Very marked variations were found together with great curtailment of productivity, some of the most susceptible varieties being complete failures.

It is the purpose in this paper to describe more fully the various phenomena found in studies of rust infection and development on certain varieties of beans, especially under greenhouse conditions.

EXPERIMENTAL METHODS

Considerable preliminary work was devoted to the development of a technic. A standard dosage, method of inoculation, and uniformity in the records of infection were recognized as some of the first requisites. One of the greatest difficulties in this connection lies in the material itself. The pathogene, together with other Uredinales, can not be grown apart from the living host, and in consequence the pure culture

[1] MILBRATH, D. C. [FIELD NOTES.] *In* U. S. Dept. Agr. Bur. Plant Indus. Off. Cotton, Truck, Forage Crop Disease Inves. News Notes, v. 7, no. 22, p. 5. 1918. Mimeographed.

standards of the bacteriologist can only be approximated. The strain of the fungus used in the experimental work to be discussed was obtained from Kentucky Wonder beans in a garden at Blacksburg in the fall of 1917. In an effort to obtain a single spore strain, bean plants were inoculated sparingly with urediniospores, and only a few well-isolated sori were obtained. Urediniospores from a single sorus were used again for a sparing inoculation on other plants. The repetition of this procedure through several spore generations provided a strain which could, with reasonable certainty, be considered to have arisen from a single urediniospore. Stock cultures of this strain were maintained on plants of Tennessee Green Pod, and all of the inoculum used was taken from this variety.

The method of inoculation used throughout the work consisted in the atomization of the host with a urediniospore suspension followed by incubation in a moist chamber for 24 hours. One of the authors (*3*) in studies with the crownrust of oats had found that the best infection was obtained when dry spores from a culture of rusted oat seedlings were allowed to fall on plants which had been previously atomized with water. Melhus and Durrell (*8*) have also found dusting the spores on the moistened plants preferable to the use of spore suspensions. They have found a considerable reduction in the percentage of germination of urediniospores of this rust after passing them through an atomizer. There seems, however, to be greater probability of securing uniformity of dosage with spore suspensions, and this method has, therefore, been followed in our work.

A standard dosage was used throughout the experiments, the inoculum for each plant being the spores from one mature uredinium, grown on Tennessee Green Pod, applied in 1 cc. of water. In practice 40 plants were inoculated at one time, the dosage being the urediniospores from 40 sori in 40 cc. of water.

Since it had been determined previously that the susceptibility of the bean leaf varies somewhat according to the degree of maturity, the inoculations were made with the plants in as near the same stage of development as possible, the rule followed being to select the time when the first trifoliate leaf had reached a length of about ½ inch. At this time the primordial leaves have attained practically their full size but are still young and in a susceptible state. The number of days required to reach this stage of development from the planting of the seed varies with the conditions in the greenhouse between 11 and 20 days, averaging about 14 days.

In order to secure uniformity of exposure to infection an inoculation frame is employed to hold 40 four-inch pots each of which contains a single bean plant. Four varieties are inoculated in each test, 10 plants to a variety, the varieties being distributed through the frame in such a

manner as to overcome any inequality in inoculation. Plate 69, A, shows the frame filled in preparation for inoculation. The inoculum, as stated previously, is applied with an atomizer, all plants receiving as nearly as possible the same amount of material. A very fair degree of uniformity in the resultant infection is obtained as a rule by this method throughout the 10 plants of a variety. The results of one test are shown in Table I.

TABLE I.—*Experiment No. 29. Results of inoculation of four varieties of beans planted December 9 and inoculated December 31 at the rate of one sorus per plant; sori visible January 8, sporulating January 10; count made January 17*

Plant No.	Tennessee Green Pod.						McCaslan.					
	Leaf No. 1.			Leaf No. 2.			Leaf No. 1.			Leaf No. 2.		
	Number of sori.	Number of flecks.	Area.	Number of sori.	Number of flecks.	Area.	Number of sori.	Number of flecks.	Area.	Number of sori.	Number of flecks.	Area.
			Square inches.			*Square inches.*			*Square inches.*			*Square inches.*
1	206	.....	8. 73	213	.....	8. 47	452	.....	10. 64	194	.....	9. 37
2	134	.....	5. 32	86	.....	5. 19	310	.....	8. 53	319	.....	7. 90
3	180	.....	6. 33	90	.....	6. 14	225	.....	10. 60	281	.....	9. 52
4	299	.....	6. 00	269	.....	5. 17	205	.....	5. 23	221	.....	5. 72
5	132	.....	5. 98	209	.....	5. 47	142	.....	5. 35	163	.....	4. 95
6	337	.....	6. 23	156	.....	6. 03	400	.....	6. 60	191	.....	5. 97
7	113	.....	5. 30	247	.....	5. 96	286	.....	6. 98	257	.....	7. 03
8	245	.....	6. 10	240	.....	6. 63	278	.....	6. 00	302	.....	6. 40
9	102	.....	3. 98	178	.....	4. 55	356	.....	5. 40	352	.....	5. 60
10	133	.....	4. 47	144	.....	4. 29	263	.....	6. 80	134	.....	6. 20
Total	1,880	.....	58. 44	1,832	.....	57. 90	2,917	.....	72. 13	2,414	.....	68. 66

Plant No.	Improved Goddard.						Dwarf Black.					
	Leaf No. 1.			Leaf No. 2.			Leaf No. 1.			Leaf No. 2.		
	Number of sori.	Number of flecks.	Area.	Number of sori.	Number of flecks.	Area.	Number of sori.	Number of flecks.	Area.	Number of sori.	Number of flecks.	Area.
			Square inches.			*Square inches.*			*Square inches.*			*Square inches.*
1	.....	196	10. 90	.....	158	11. 80	44	42	4. 57	26	25	4. 40
2	.....	140	10. 78	.....	78	12. 00	47	39	7. 70	36	30	7. 69
3	.....	76	8. 78	.....	82	8. 97	47	39	4. 50	47	19	5. 69
4	.....	106	9. 45	.....	53	10. 40	50	17	3. 75	17	9	3. 90
5	.....	148	13. 79	.....	137	14. 13	9	3	5. 68	31	12	4. 43
6	.....	118	11. 55	.....	179	12. 15	30	28	4. 15	10	4	4. 60
7	.....	136	11. 37	.....	93	10. 55	10	10	4. 93	14	16	3. 94
8	.....	71	13. 85	.....	179	13. 90	31	20	7. 10	65	22	6. 75
9	.....	91	9. 86	.....	92	9. 70	49	31	5. 80	41	34	6. 35
10	.....	139	15. 50	.....	139	15. 54	36	32	5. 07	28	20	5. 04
Total	.....	1,221	115. 83	.....	1,190	119. 14	353	261	53. 25	315	191	52. 79

TABLE II.—*Summary of experiment No. 29. Percentage of total infection and fertile infection in terms of Tennessee Green Pod, which is taken as the standard and rated 100 per cent*

	Tennessee Green Pod.	McCaslan.	Improved Goddard.	Dwarf Black.
Total number of sori on 20 leaves	3,712	5,331	.....	668
Total number of flecks on 20 leaves	.....	.....	2,411	452
Total number of infections on 20 leaves	3,712	5,331	2,411	1,120
Total area in square inches	116.34	140.79	234.97	106.04
Number of sori per square inch	31.91	37.87	.....	6.30
Number of flecks per square inch	.....	.....	10.26	4.26
Number of infections per square inch	31.91	37.87	10.26	10.56
Percentage of total infection	100.00	118.68	32.15	33.09
Percentage of fertile infection	100.00	118.68	.....	19.74
Percentage of abortive infection [1]	.....	.....	100.00	40.36

[1] Calculated from total infection on each variety separately.

Following inoculation the plants are removed to a moist chamber large enough to hold all 40 plants. They are kept here in a humid atmosphere for 24 hours and are then set on the greenhouse bench. The incubation period varied within limits of 8 to 14 days during the tests, the average time from inoculation to the rupture of the sorus being 10 days. The sori are visible two or more days prior to sporulation. The final data on infection are secured 7 days after sporulation begins. This permits a full development of the initial infection on all varieties but comes early enough to exclude secondary sori which develop around the primary sorus in the more susceptible varieties (Pl. 71, B). At this time the primordial leaves are removed from the plants and the number of infections (both sori and flecks) are determined. The typical infection obtained on susceptible varieties is shown on a leaf of Dutch Case Knife in Plate 70, A, and abortive infection or flecking on a leaf of Improved Goddard in Plate 70, B.

A photographic retouching frame has been found a great aid in the counting of infections. The leaves are placed on a glass plate in this frame before an incandescent lamp, and by this lighting it is possible to determine the number of infections on both leaf surfaces at the same time, thus preventing the duplication which would result from separate counts. Infection takes place with equal readiness on both upper and lower surfaces, but with the method of inoculation used the greater number develop on the upper surface. In many cases the sorus breaks through on both surfaces. Before the count is taken the leaf surfaces are brushed with a camel's-hair brush to remove dirt and superfluous spore powder. Following the count the area of the leaf is determined by means of a planimeter, and the number of infections is reduced to a unit area basis in all varieties.

VARIATION IN DEVELOPMENT OF INFECTION

The normal development on the more susceptible varieties, of which Tennessee Green Pod is an example, is described as follows from inoculation made on January 20, 1919. The inoculation was made at 5 p. m., and after 24 hours in the moist chamber the plants were placed on the greenhouse bench. The first evidence of infection was noted 136 hours after inoculation. The sori at this time were very faint indeed, being scarcely visible. In 143 hours they were evident on close examination as minute pale spots. They were quite distinct after 161 hours, had taken on a pale yellow color, and were slightly elevated above the leaf surface. At 183 hours the centers of the sori were orange-red in color, showing sporulation, and were conspicuously elevated. The epidermis had ruptured on some of the larger sori in 190 hours, and the uredinio-spores were exposed. A ring of secondary sori develops around the primary sorus on the more susceptible varieties.

Variations from the normal development are found in a number of varieties. These variations may be listed as follows: (a) production of flecks, (b) production of telia instead of uredinia, or sori containing both uredinio-spores and teliospores, (c) production of uredinia subnormal in size, (d) lengthening of incubation period.

The term fleck is used to indicate an abortive infection. The flecks produced on different varieties vary somewhat in shape and size (Pl. 73, A, B). The flecks which develop on Tennessee Wonder (Pl. 73, C) are seen on both leaf surfaces, but are most conspicious on the lower surface. They are circular in outline, with a slightly irregular border. The spot is concave, the tissue being noticeably shrunken. A definite bronze-brown rim bounds the fleck. This is narrow in some flecks and may extend well toward the center in others. An island of green tissue may remain in the center, and this may protrude slightly, suggesting the beginning of a sorus. In some varieties a small sorus is developed in the center of some of the flecks (Pl. 69, B, *e*, *f*). The flecks on any variety are usually larger than the sori, their average diameter being from two to three times that of the sori.

The development of flecks is characteristic of certain varieties and is considered an indication of resistance. No flecks have ever been seen on Tennessee Green Pod or other very susceptible varieties, but they are regularly produced on certain others, notably Tennessee Wonder, Improved Goddard, and Hodson Green Pod. On some varieties all the infections develop into flecks, while on others there may be a considerable number of normal sori developed and only a few flecks. The percentage of flecking with the different varieties is shown in Table III.

TABLE III.—*Susceptibility of different varieties of beans to rust infection, with infection on Tennessee Green Pod as standard and rated 100 per cent*

BUSH BEANS, GREEN POD

Experiment No.	Variety.	Average leaf area.	Number of infections per square inch.		Percentage of infection.		
			Flecks.	Sori.	Total.	Abortive.	Fertile.
		Square Inches.					
12a	Pink	4.52	.....	9.82	119.61	.....	119.61
27	Snowflake	2.67	.....	38.86	116.31	.....	116.31
27	Navy Pea	2.51	.....	36.92	110.50	.....	110.50
10	Tepary	2.28	.....	7.79	101.43	.....	101.43
5	Pinto	4.43	.....	65.88	89.20	.....	89.20
24	Lady Washington	4.05	1.87	28.76	79.10	6.12	73.83
8	Red Valentine	4.42	.....	55.09	57.29	.....	57.29
31	Blue Pod Navy	3.65	.....	05	43.60	.....	43.60
7	Red Kidney (Wells)	10.58	.....	45.76	39.39	.....	39.39
4	Emerald Beauty	10.47	.56	10.55	38.52	5.04	36.58
20	White Kidney	8.41	.....	11.34	33.35	.....	33.35
21	Burpee's Stringless	6.69	8.10	12.62	53.01	39.05	32.28
7	Full Measure	12.29	.....	37.19	32.01	.....	32.01
15	White Marrow	6.23	.....	2.92	25.15	.....	25.15
19	Warren	11.86	3.16	4.91	32.77	39.19	19.94
9	Horticultural, Dwarf	7.34	7.47	41.37	22.40	15.29	18.97
19	Round Six Weeks	6.86	.....	3.58	14.54	.....	14.54
14	French's Horticultural	8.98	1.15	2.96	16.36	27.91	11.78
18	Bountiful	8.24	1.00	1.69	13.96	36.68	8.77
34	Bird Eye	6.31	.....	.86	8.62	.....	8.62
32	Yellow Eye	9.54	.....	.69	6.97	.....	6.97
10	Longfellow	8.65	.....	.50	6.50	.....	6.50
24	Giant Stringless	7.69	.....	1.94	4.98	.....	4.98
8	Black Valentine	4.88	19.59	1.15	21.57	94.47	1.19
12a	Mexican Red	6.79	.16	.02	2.19	87.50	.24
24	Early Refugee	7.07	.84	.02	2.21	97.52	.05
14	Low's Champion	6.68	1.68	.01	6.73	99.51	.04
29	Improved Goddard	11.75	10.26	.....	32.15	100.00	.....
33	May Queen	6.25	1.97	.....	10.83	100.00	.....
18	Early Mohawk	11.86	1.95	.....	10.12	100.00	.....
18	Refugee	5.99	1.51	.....	7.83	100.00	.....
30	Hodson Green Pod	12.13	1.14	.....	5.81	100.00	.....

BUSH BEANS, WAX POD

2	Keeney's Rustless	6.97	6.51	12.03	38.89	35.15	25.24
29	Dwarf Black	5.30	4.26	6.30	33.09	40.36	19.74
33	Scarlet Wax	10.13	.66	2.23	15.88	23.11	12.25
2	Currie	8.22	18.78	1.84	43.26	91.09	3.17
23	California	6.38	10.18	.....	63.46	100.00	.....
22	Webber	7.06	12.47	.....	50.71	100.00	.....
22	Flagolet	7.28	12.18	.....	49.53	100.00	.....
26	Crystal White	3.10	5.19	.....	44.24	100.00	.....
23	Challenge	4.91	4.80	.....	29.93	100.00	.....
22	Wardwell	6.65	6.58	.....	26.76	100.00	.....
23	New Pearl	7.56	3.22	.....	20.07	100.00	.....
27	Hodson Wax	6.68	5.88	.....	17.60	100.00	.....
23	Detroit	8.57	1.85	.....	11.53	100.00	.....
26	Golden Eye	8.31	1.08	.....	9.21	100.00	.....

TABLE III. *Susceptibility of different varieties of beans to rust infection, with infection on Tennessee Green Pod as standard and rated 100 per cent*—Continued

POLE BEANS, GREEN POD

Experiment No.	Variety.	Average leaf area.	Number of infections per square inch.		Percentage of infection.		
			Flecks.	Sori.	Total.	Abortive.	Fertile.
		Square inches.					
29	McCaslan	7.04	.....	37.87	118.68	.....	118.68
20	Virginia Cornfield	4.11	.....	36.07	106.09	.....	106.09
32	Cut Short	5.30	.....	3.19	104.61	.....	104.61
11	Kentucky Wonder	7.46	.....	5.75	80.87	.....	80.87
28	Dutch Case Knife	5.89	.....	36.85	77.50	.....	77.50
9	Royal Corn	5.03	.....	146.04	66.97	.....	66.97
26	Powell's Prolific	5.90	.....	6.82	58.14	.....	58.14
28	Creaseback	4.03	.....	24.32	51.12	.....	51.12
1	Lazy Wife	7.21	.....	2.68	13.74	.....	13.74
1	Horticultural, Pole	9.78	.....	2.12	10.87	.....	10.87
13a	Brockton	10.95	0.21	.05	6.77	80.70	1.31
7	Tennessee Wonder	10.09	63.10	.68	54.91	98.93	.59
13a	Marblehead	8.76	.10	.01	2.86	90.00	.26
	POLE BEANS, WAX POD						
17	Golden Cluster	5.84	.....	4.80	71.22	.....	71.22
28	Kentucky Wonder Wax	5.73	.....	32.32	67.94	.....	67.94
21	Mont d'Or	9.60	3.81	.....	9.75	100.00	.....
20	Everbearing	9.80	.45	.....	1.32	100.00	.....
17	Indian Chief	10.52	.....	.....	.....	.....	.....

In general the flecks are visible some time before the sori are evident. Accompanying the inoculation of Tennessee Green Pod on January 20, described previously, in which 143 hours elapsed before the "anlage" of the sori were plainly visible, flecks were visible on Hodson Green Pod in 112 hours and on Improved Goddard and Tennessee Wonder in 123 hours.

On certain varieties the immediate results of the inoculation with urediniospores is seen in the production of telia or of mixed sori. This is particularly true of Black Valentine and of some of the wax-podded varieties, notably Challenge, Flagolet, Golden Eye, Pencil Pod, Keeney, Wardwell, and New Kidney.

The size of uredinia will vary to some extent on a given variety according to the degree of infection and crowding. The average size of the sorus on different varieties varies greatly, however, ranging from about 180 μ on Dwarf Black Wax to 600 μ on Tennessee Green Pod (compare A and B, Pl. 72, and *a* and *d*, Plate 69, B).

The duration of the incubation period is modified by environment, especially temperature, but in different varieties under similar conditions a variation of several days may occur. Such variations have

been noted repeatedly. In order to have more definite data on this point two plants each of 72 varieties were inoculated on March 29, 1920, and were held under similar conditions. Thirty-seven of the varieties produced uredinia only, 3 both uredinia and flecks, 27 flecks only, and 5 neither sori nor flecks. The number of days elapsing before the uredinial "anlage" were visible varied from 6 to 10 on different varieties, and the time of sporulation from 10 to 15 days. The "anlage" were visible on 6 varieties on the sixth day, on 9 varieties on the seventh day, on 22 varieties on the eighth day, on 1 on the ninth day, and on 2 on the tenth day. Sporulation ensued on 6 varieties on the tenth day, on 30 on the eleventh day, on 2 on the twelfth day, on 1 on the fourteenth, and on 1 on the fifteenth. The number of days between the appearance of the "anlage" and sporulation varied from two to five, the mean being three days. As a general rule the sorus develops more rapidly on the more susceptible varieties than on the more resistant. The flecks on the resistant varieties were visible, as a rule, sooner than the "anlage" on the susceptible varieties. Flecks were observed on 9 varieties on the fifth day, on 16 on the sixth day, on 4 on the seventh, and on 1 on the eighth.

RELATIVE SUSCEPTIBILITY OF BEAN VARIETIES

In our previous publication (*4*) a number of varieties of beans were classified according to their susceptibility to rust under field conditions. Four classes were recognized—rust-free, rust-proof, rust-enduring, and rust-susceptible. In this work we have attempted to obtain a more definite expression of susceptibility by using a susceptible variety as a standard and expressing the relative susceptibility of other varieties in terms of that standard. A standard dosage is employed and the relative susceptibility of a variety is indicated by the percentage of infection obtained, modified by the amount of flecking, the size of the sorus, and the length of the incubation period.

The determination of the degree of infection is based on the assumption that all varieties receive approximately the same number of urediniospores per unit area of leaf surface exposed as the standard. The resultant infection is then determined by count and is calculated as average number of infections per square inch. The number of sori obtained on Tennessee Green Pod is then rated 100 per cent, and the number of infections on the other varieties in the test is reduced to percentage of the standard. The percentage of infection is expressed as total infection (both sori and flecks), fertile infection (sori only), and abortive infection (flecks). Total infection and fertile infection are in terms of the standard, but abortive infection relates only to the variety in question and is the percentage of the total infections aborted on that variety. The details of this method are illustrated in Tables I and II. Table III is a summary of the experiments and shows the degree of infection obtained on the 64 varieties tested.

The varieties are grouped for convenience according to the dwarf or running habit and the color of the pod. Of the 46 varieties of dwarf or bush beans, 32 have green pods and 14 wax pods. Of the 18 varieties of pole beans, 13 have green pods and 5 wax pods.

The very marked variation in the susceptibility of the different varieties under the conditions of the experiments is evident. They are arranged in the different groups according to susceptibility to infection, the production of sori (percentage of fertile infection) being used as the basis for comparison in those varieties which produce sori rather than the percentage of total infection.

In Table IV the 64 varieties are grouped under the four classes, and the comparative susceptibility of the classes as a whole is shown. It is apparent that pole beans with green pods constitute the most susceptible class and bush beans with wax pods the least susceptible, that pole beans are more susceptible as a class than bush beans, and that green-pod varieties are more susceptible than wax-pod varieties.

Considering that the production of sori is an indication of greater susceptibility than the production of flecks, it is seen that 67 per cent (12 in 18) of the pole varieties produced sori unaccompanied by flecks as compared with 35 per cent (16 in 46) of the bush beans, while only 11 per cent of the former class produced flecks unaccompanied by sori as compared with 33 per cent of the latter class. Comparing green-pod varieties with wax-pod varieties, the percentage with sori only is 58 as against 11, and for flecks only the percentage is 11 as against 63. Comparing severity of infection on individual varieties, it is seen that the fertile infection was 50 per cent or more of the standard in 55 per cent of the pole varieties as against 15 per cent of the bush varieties, and in 33 per cent of the green pods as against 11 per cent of the wax pods.

TABLE IV.—*Susceptibility of different classes of bean varieties to rust*

	Bush.		Pole.	
	Green.	Wax.	Green.	Wax.
Number of varieties tested	32	14	13	5
Number bearing sori only	16	.....	10	2
Number bearing sori and flecks	11	4	3	.....
Number bearing flecks only	5	10	.....	2
Number showing no infection	.....	.....	.....	1
Number showing fertile infection 50 per cent or more of standard	7	.....	8	2

CORRELATION BETWEEN SEED CHARACTERS AND SUSCEPTIBILITY TO RUST

In order to determine whether susceptibility to rust is associated with any particular color pattern or shape of the seed, a study of the seed

characters of a number of varieties was made. The data on seed characters have been drawn largely from Jarvis (*6*), supplemented by observations when necessary. The details of this study are shown in Table V. Only two classes with respect to susceptibility are provided, the rust-enduring, rust-proof, and rust-free varieties all being classed as resistant. Although it is probably impossible to draw conclusions that would not be subject to exceptions, nevertheless the following general statements can be made for the 51 varieties included in the study. With respect to color, all solid red or red mottled beans are rust-resistant. With respect to shape, all marrow beans are rust-resistant. White beans seem to be more susceptible as a group than black or brown beans, and pea beans more so than medium or kidney.

VARIABILITY OF VARIETIES

It is of interest to note to what extent the individual plants of a variety differ in behavior to rust infection. Although the number of plants of a variety under observation in the experiments is not large enough to justify more than tentative conclusions, sufficient additional evidence from field trials is available to indicate that the stability or variability of a variety as indicated below is approximately correct. The majority of varieties studied were stable with respect to rust infection, all individuals responding in the same way. The standard used, Tennessee Green Pod, is especially reliable in this respect. Of the 340 plants inoculated in the experiments all developed sori, and not a single fleck was observed. The stable varieties are grouped as follows, according to the character of the response to inoculation.

TABLE V.—*Correlation between seed characters and susceptibility to rust*[1]

Color of seed.	Pea.	Medium.	Marrow.	Kidney.	Totals.
White	2/7	1/2	2/2	1/5	6/16
White, yellow eye	.....	.....	2/2	.....	2/2
Black	.....	2/3	1/1	.....	3/4
Brown	.....	1/1	2/2	3/5	6/8
Yellow, brown ring	.....	1/1	.....	1/1	2/2
Red	.....	.....	4/4	1/1	5/5
Red on fawn or buff ground	.....	.....	3/3	5/5	8/8
Pink	.....	0/1	.....	.....	0/1
Brown, purple, or black on fawn or buff ground.	.....	0/1	.....	4/4	4/5
Total	2/7	5/9	14/14	15/21	36/51

[1] The denominator shows the total number of varieties, the numerator the number that are rust-resistant.

ALL PLANTS PRODUCING SORI ONLY, NO FLECKS.—Pink, Snowflake, Navy Pea, Tepary, Pinto, Red Kidney, White Kidney, Full Measure, Round Six Weeks, Longfellow, Giant Stringless, McCaslan, Virginia Cornfield, Cut Short, Kentucky Wonder, Dutch Case Knife, Royal Corn, Powell's Prolific, Creaseback, Golden Cluster, and Kentucky Wonder Wax.

ALL PLANTS PRODUCING FLECKS ONLY, NO SORI.—Refugee, Early Mohawk, May Queen, Improved Goddard, California, Webber, Flagolet, Challenge, Wardwell, New Pearl, Hodson Wax, Detroit, Golden Eye, and Mont d'Or.

ALL PLANTS PRODUCING BOTH SORI AND FLECKS, THE SORI BORNE EITHER WITHIN THE FLECKS OR INTERMIXED WITH THEM.—Dwarf Black Wax, Burpee's Stringless, Tennessee Wonder, and Black Valentine.

ALL PLANTS CLEAN, PRODUCING NEITHER SORI NOR FLECKS.—Indian Chief.

The individual plants of the remaining 25 varieties were somewhat variable in response to rust inoculation. This is shown in Table VI. In the varieties Blue Pod Navy, Yellow Eye, Lady Washington, White Marrow, and Bird Eye, a large percentage of the individuals developed sori and a small percentage showed no infection, while these conditions were reversed in Lazy Wife. There were no intermediate or flecking plants in any of these.

TABLE VI.—*Response of individual plants of unstable varieties to rust inoculation*

Variety.	Percentage of plants showing—			
	Sori only.	Sori and flecks.	Flecks only.	Clean.
Blue Pod Navy	95	.....	.....	5
Yellow Eye	95	.....	.....	5
Emerald Beauty	90	10	.....	.....
Lady Washington	90	.....	.....	10
White Marrow	90	.....	.....	10
Bird Eye	90	.....	.....	10
May Queen	60	40	.....	.....
Horticultural Pole	55	5	5	35
Bountiful	50	25	25	.....
Horticultural Dwarf	45	.....	5	50
Red Valentine	40	55	.....	5
Warren	35	10	55	.....
French's Horticultural	30	70	.....	.....
Keeney	30	70	.....	.....
Brockton	20	.....	50	30
Currie	10	65	25	.....
Early Refugee	10	10	60	20
Marblehead	10	10	40	40
Mexican Red	10	.....	50	40
Lazy Wife	5	.....	.....	95
Scarlet Wax	.....	90	10	.....
Low's Champion	.....	40	60	.....
Hodson Green Pod	.....	5	95	.....
Everbearing	.....	.....	20	80

The greatest variability is shown in the varieties Horticultural Pole, Horticultural Dwarf, Brockton, Early Refugee, Marblehead, and Mexican Red. All had a considerable percentage of clean plants, some that developed sori, and some intermediates.

SIZE OF THE SORUS AS AN INDEX OF SUSCEPTIBILITY

In addition to the degree of infection and the production of flecks, the size of the sorus produced on different varieties also provides an index of relative susceptibility. As noted previously, great variation exists in the size of the sori produced on different varieties. The size of the sorus in turn is an index to the spore production of the sorus, and any marked curtailment in the number of spores produced may readily be conceived to be a limiting factor of considerable importance in the propagation of the pathogene. The production of a small sorus is evidently to be considered in the same light as the production of flecks—as a response to an unfavorable medium.

The average size of the uredinium on each variety has been determined by measurement of a number of uredinia. The relative spore-producing capacity is then determined by calculating the number of urediniospores produced in a layer one spore in thickness covering the sorus. This does not represent the total spore-producing capacity of the sorus but gives a basis for comparison between varieties. The main objection to this expression is that it does not magnify the differences between the more susceptible and more resistant varieties sufficiently. It seems evident from examination that the more susceptible varieties produce more layers of spores in a uredinium than the more resistant ones. No differences have been found in the size of the urediniospores borne on different varieties.

In determining the number of spores produced by a sorus, the number in the diameter is determined by calculation. The urediniospore is approximately 20 μ in diameter, and 30 such spores would be contained in the diameter of a sorus 600 μ broad. The square of the number in the diameter multiplied by 0.7854 gives the number in one layer covering the sorus. The sorus on Tennessee Green Pod, which is one of the largest, averages 600 μ in diameter and, therefore, has a spore-producing capacity of 706.8 spores in one layer, while that on Bird Eye, averaging 300 μ, has a spore-producing capacity of only 176.7. The spore-producing capacity of the sorus on different varieties has been reduced to percentages for purposes of comparison. The sorus on Tennessee Green Pod is again used as the standard, and its spore-producing capacity is rated 100 per cent. The varieties on which data were obtained are grouped in Table VII according to spore production.

It will be noted in a comparison between Tables VII and III that varieties with high rating in percentage of fertile infection also show rate high in spore-producing capacity. Tepary is the only variety rating above 50

per cent in fertile infection which falls below 50 per cent in spore-producing capacity, while three varieties, White Marrow, Full Measure, and Keeney's Rustless, rating below 50 per cent in fertile infection, have spore-producing capacities in excess of 50 per cent. In general it can be stated that the production of large sori is an indication of greater susceptibility to infection than the production of small sori.

TABLE VII.—*Relative spore-producing capacity of the uredinia on different varieties*

Spore-producing capacity.		Variety.
Per cent.	Number.	
100	707	Tennessee Green Pod, Navy Pea, Snowflake, Lady Washington, McCaslan, Virginia Cornfield, Dutch Case Knife, Powell's Prolific, Creaseback, Cut Short, Golden Cluster.
70	491	Pinto, White Marrow, Kentucky Wonder, Royal Corn.
54	380	Pink, Red Valentine, Full Measure, Keeney's Rustless.
44	314	Tepary, Blue Pod Navy, Red Kidney, White Kidney, Horticultural Dwarf, Round Six Weeks, Longfellow, Low's Champion, Brockton, Tennessee Wonder, Kentucky Wonder Wax.
32	227	Early Refugee, Giant Stringless, Bountiful, Horticultural Pole.
25	177	Warren, Bird Eye, French's Horticultural, Black Valentine, Marblehead, Currie.
16	113	Yellow Eye, Burpee's Stringless, Mighty Nice, Mexican Red.
11	79	Scarlet Wax, Crystal White, Dwarf Black.

SUSCEPTIBILITY OF BEAN VARIETIES UNDER GREENHOUSE CONDITIONS AS COMPARED WITH FIELD CONDITIONS

The question is naturally raised in connection with greenhouse experiments as to what extent they serve as a reliable index of field behavior. All the varieties of beans used in our greenhouse work have been grown in the field, most of them during two seasons, where they have been subjected to uniform exposure to rust infection by inoculation. The results of the first season's field tests have been described in a previous paper (*4*). In the 1918 tests the varieties were classified according to relative susceptibility in four groups, as follows: Susceptible, rust-enduring, rust-proof, rust-free. Yields were obtained only for the dwarf varieties commonly grown for dry-shell purposes and from the pole beans. In the 1919 tests some of the most susceptible varieties were eliminated and some additional varieties were added. This season was particularly favorable for the development of anthracnose, and some of the varieties suffered severe losses from this disease and to a lesser degree from bacterial blight. With respect to rust infection, the varieties respond in the same way during the two seasons, but the effects

of the rust attack were not so noticeable in 1919 as in 1918. The susceptible varieties were severely rusted, but defoliation was not so severe until later in the season, and their yield was better in comparison with that of the more resistant varieties than in 1918. No data on the curtailment of the yield of the pole varieties as determined by rust infection could be obtained because of the severity of anthracnose on certain varieties.

The greenhouse and field behavior of the dry-shell varieties is compared in Table VIII, and that of the pole varieties in Table IX. The varieties are listed according to susceptibility in the greenhouse.

Of the 17 varieties in Table VIII the first 7, which were classed as susceptible in the field, all rated above 70 per cent fertile infection in the greenhouse, while the 9 varieties in the resistant classes—enduring, proof, and free—all fell below 50 per cent fertile infection. Robust, not included in the greenhouse tests, was classed as rust-proof in the field and outyielded all other varieties in 1919. This is the only small white bean in our tests, with the exception of Blue Pod Navy, which has successfully withstood the attack of rust. Robust seems to be an especially desirable variety in that it combines resistance to mosaic, as shown by Reddick and Stewart (*9*), with rust resistance, attractive appearance, and desirable commercial type. Bird Eye, grown for the first time in 1919, was classed as rust-free and was second to Robust in yield. This variety is similar to Yellow Eye in seed characters and is popular in some localities in Virginia. It is attractive and of good quality and seems to be very dependable. The yields in 1918 are more representative of the curtailment of production by rust than those in 1919, since anthracnose was severe in the latter year. The yields of Improved Goddard, Horticultural Dwarf, and White Kidney were reduced materially by anthracnose. Bird Eye and Well's Red Kidney were especially free from anthracnose. Robust was quite free from anthracnose in 1919 but was severely injured in 1920.

Of the 18 varieties of pole beans listed in Table IX the 8 which were classed as susceptible all exceeded 50 per cent fertile infection in the greenhouse. All the rust-proof and rust-free varieties fell below 50 per cent; but the two rust-enduring varieties, Golden Cluster and Kentucky Wonder Wax, rated 71 and 68 per cent. The yield of all of the susceptible varieties was severely curtailed by the rust attack in 1918, 5 of them being complete failures (Pl. 71, A). McCaslan was not grown in 1918 but was seriously damaged in 1919. No yield data for 1919 are given, as explained previously, because of the severity of anthracnose. This injury was especially severe on Indian Chief, Everbearing, Mont d'Or, Marblehead, Brockton, and Lazy Wife.

TABLE VIII.—*Comparison between greenhouse and field behavior of dry-shell beans*

Variety.	Percentage of fertile infection in greenhouse.	Field.			
		Susceptibility to rust.	Yield of dry beans.		Severity of anthracnose.
			1918.	1919.	
			Gm.	*Gm.*	
Pink	120	Susceptible	[a] 14	.....	
Snowflake	116	.....do.....	[a] 386	.....	
Navy Pea	111	.....do.....	[a] 313	[a] 2,390	Slight.
Tepary	101	.....do.....	[a] 0	.....	
Tennessee Green Pod	100	.....do.....	[a] 270	.....	
Pinto	89	.....do.....	[a] 153	.....	
Lady Washington	74	.....do.....	[a] 633	[a] 2,174	Do.
Robust	(c)	Proof	.....	9,976	None.
Blue Pod Navy	44	Enduring	1,121	4,370	Moderate.
Red Kidney	39	Free	1,852	4,085	None.
White Kidney	33	.....do.....	682	[b] 2,960	Severe.
White Marrow	25	Enduring	1,119	4,024	Slight.
Horticultural Dwarf	19	Proof	1,305	[b] 2,730	Very severe.
Bird Eye	9	Free	.....	4,918	None.
Yellow Eye	7	Proof	938	3,250	Slight.
Mexican Red	−1	Free	1,090	3,185	Moderate.
Improved Goddard	−1	.....do.....	618	[b] 1,310	Very severe.

[a] Yield reduced materially by rust.
[b] Yield reduced materially by anthracnose.
[c] Not tested.

TABLE IX.—*Comparison between greenhouse and field behavior of pole beans*

Variety.	Percentage of fertile infection.	Field rating.	Yield in 1918.	Severity of anthracnose in 1919.
			Gm.	
McCaslan	119	Susceptible	.....	Slight.
Virginia Cornfield	106	.....do.....	0	
Cut Short	105	.....do.....	0	
Kentucky Wonder	81	.....do.....	109	Moderate.
Dutch Case Knife	78	.....do.....	159	Slight.
Golden Cluster	71	Enduring	263	Do.
Kentucky Wonder Wax	68	.....do.....	216	Do.
Royal Corn	67	Susceptible	0	
Powell's Prolific	58	.....do.....	0	Do.
Creaseback	51	.....do.....	0	
Lazy Wife	14	Variable	.....	Very severe.
Horticultural Pole	11	Proof	897	Slight.
Brockton	1	Free	556	Very severe.
Tennessee Wonder	−1	Proof	751	
Marblehead	−1	Free	371	Severe.
Mont d'Or	0	.....do.....	506	Very severe.
Everbearing	0	.....do.....	143	Do.
Indian Chief	0	.....do.....	261	Do.

There is in general a very satisfactory agreement between the greenhouse and field behavior of bean varieties; and the greenhouse test, properly interpreted, seems to afford a reliable basis for predicting the

relative susceptibility of a variety in the field. The greenhouse test is seemingly a more severe one than the field test. Some varieties which have developed a few sori in the greenhouse have remained entirely rust-free in the field. It seems to hold true that a variety which develops less than 50 per cent fertile infection in the greenhouse does not suffer material injury from rust in the field, and conversely that a variety which exceeds 50 per cent infection in the greenhouse may be expected to suffer material injury in the field. No exceptions to the first rule have been noted and only two apparent exceptions, Golden Cluster and Kentucky Wonder Wax, to the latter. Both these varieties were conspicuously rusted in the field, but both yielded fair crops. It is impossible to state the degree of injury sustained by these varieties, since no rust-free plants were available for comparison.

CURTAILMENT OF YIELD DUE TO BEAN RUST

Attempts have been made to obtain data on the amount of reduction in yield caused by bean rust, but the nature of the pathogene makes the securing of reliable data almost impossible. Yield data from rusted and rust-free plants should preferably be obtained from alternating rows in the same plot, but it is impossible to maintain rust-free plants of susceptible varieties in the same plot with rusted plants. It was thought that the difficulty might be overcome by growing both resistant and susceptible varieties in separate isolated rusted and rust-free plots, the resistant varieties being used as a criterion of the relative crop-producing capacities of the different soils.

A planting of this type was made in 1918 with Improved Goddard as the resistant variety and Navy Pea and Tennessee Green Pod as the susceptible varieties. The soil of the two plots was similar in physical properties and apparently so in fertility. All plants in the rusted plot were inoculated with urediniospores, and a general and severe infection resulted on the rows of susceptible varieties. The rust-free plot was not inoculated. It became infected naturally later in the season but not early enough to cause any material reduction in yield. Unfortunately the rust-resistant variety was so severely attacked by anthracnose that no reliable yield data could be obtained. The difference in growth and yield of the rust-susceptible varieties on the two plots was very marked, almost no beans being produced in the rusted plot. The yields of shelled beans for single rows 65 feet in length were as follows: Tennessee Green Pod, rust-free plot 267 gm., rusted plot 9 gm., difference 95 per cent; Navy Pea, rust-free plot 494 gm., rusted plot 95 gm., difference 81 per cent.

A similar test was made in 1920 with three susceptible and three resistant varieties. The two plots were on the same piece of land but were separated by a strip of corn. Rust was very abundant on the susceptible varieties in the inoculated plot, while the control remained free

throughout the season. The injury from rust was not so great as in 1918, apparently on account of seasonal differences; and the plants in the rusted plot retained their leaves longer and matured a fair crop. The yields are shown in Table X. The figures are in grams of shelled beans for single rows 60 feet in length and are averages of two rows for each variety. It will be noted that the three susceptible varieties all show a decrease in yield on the inoculated plot, while the three resistant varieties show an increase. It seems from this that the soil of the inoculated plot was better and that greater differences in the yield of the rusted and rust-free rows of susceptible varieties would be expected on plots of equal fertility. The three susceptible varieties show an average decrease of 28 per cent in the inoculated plot, while the three resistant varieties show an average increase of 31 per cent. It seems apparent that a reduction in yield of 50 per cent or more may be expected from a severe rust attack on susceptible varieties.

TABLE X.—*Yields of rust-susceptible and resistant varieties of beans in rusted and rust-free plots*

Variety.	Susceptibility to rust.	Rust-free plot.[1]	Rusted plot.[1]	Yield of rusted plot in percentage of rust-free plot.
Tennessee Green Pod	Susceptible	970	530	55
Pinto	do	385	217	56
Navy Pea	do	1,007	959	95
Bird Eye	Resistant	2,243	2,325	104
Yellow Eye	do	1,466	2,091	143
Red Kidney	do	2,162	3,256	151

[1] Expressed in grams per 60-foot row.

BIOLOGIC FORMS OF BEAN RUST

We have made no extended study of the occurrence of biologic forms of the bean-rust fungus, but it seems desirable to record such observations as have been made in connection with the studies on susceptibility of varieties.

The strain of rust from the kidney or garden bean which we have used in our studies has been tested on a large number of horticultural varieties of the kidney bean (*Phaseolus vulgaris*), on 9 varieties of the lima bean, (*P. lunatus* L.), 1 variety of the tepary bean (*P. acutifolius latifolius* D. F. Freeman), 18 varieties of cowpeas (*Vigna sinensis* (L.) Endl.), 1 variety of the broad or horse bean (*Vicia faba*), and 1 variety of asparagus bean (*Dolichos sesquipedalis* L.). Infection has resulted on many varieties of the kidney bean, as recorded previously, and also on the tepary bean. Slight infection only was obtained on 1 variety of lima bean in the greenhouse, but the other 8 varieties tested remained free from infection in both greenhouse and field. The infection in this case was slight and con-

sisted of small telia borne in the centers of flecks. No infection was obtained on the horse bean, the asparagus bean, nor on any variety of cowpea.

A second form distinct pathologically from the foregoing but similar morphologically was isolated in 1919 from leaves of cowpeas, variety Black Eye, which were sent us from California by Mr. D. C. Milbrath. It has been cultured in the greenhouse on plants of this variety and has been used for both greenhouse and field inoculations on a number of varieties of kidney beans and 18 varieties of cowpeas. Infection has been obtained on only the Black Eye variety of cowpea and on two similar strains, Extra Early Black Eye and Ramshorn Black Eye. No tests have been made on lima, horse, tepary, or asparagus beans.

These two strains may be designated the kidney-bean strain and the cowpea strain. They are distinct biologically, but their host ranges are as yet imperfectly known. It is possible that more than one biologic form occurs on kidney beans, but such evidence as is at hand would indicate that the strain which occurs commonly on kidney beans in the United States has the same host preferences as the one we have studied. The behavior of varieties in Maine, as observed by Morse (*9*), agrees in all essentials with our data, and the general mention of rust on Kentucky Wonder in other States points to this conclusion. It seems probable that a distinct biologic form occurs in South America. Gassner (*5*) records rust as severe on Mont d'Or and Flageolet, two-wax-pod varieties, while our strain produced flecks only on these. It is possible, however, that the varieties grown under these names by us were distinct from those used in South America. Gassner obtained his seed from Europe.

SUMMARY

A technic of inoculation and method of record is described which makes possible the expression of the relative rust susceptibility of varieties of beans in terms of percentage of a standard.

Variations from the behavior of the susceptible standard which occur in different varieties following inoculation with urediniospores in the greenhouse are of the following types: (*a*) reduction in number of infections, (*b*) reduction in the size of the uredinium, (*c*) abortion of infection or flecking, (*d*) immediate production of telia instead of uredinia, (*e*) lengthening of the incubation period. These variations are considered as responses to an unfavorable medium and as expressions of resistance.

Of the varieties studied, those with indeterminate growth (pole beans) were more susceptible as a class than those with determinate growth (bush beans). Green-pod varieties were more susceptible as a class than wax-pod varieties. With respect to color of seed all varieties with solid red or red mottled seed were rust resistant, while varieties with white seed were more susceptible as a class than those of any

other color. With respect to form of seed all varieties of the marrow type were rust resistant and those with pea beans constituted the most susceptible class.

Little or no variation in the susceptibility of individuals was found in the majority of the varieties studied, but marked variation existed between individuals in a few varieties.

Field tests which have supplemented the greenhouse tests have demonstrated that the greenhouse test affords a reliable index of the field behavior of a variety with respect to rust infection. An attack of rust on susceptible varieties in the field may result in a curtailment of production amounting to 50 per cent or more, and in very severe attacks to total loss.

The existence of two biologic forms of the bean-rust fungus has been demonstrated, but their host ranges are as yet imperfectly known.

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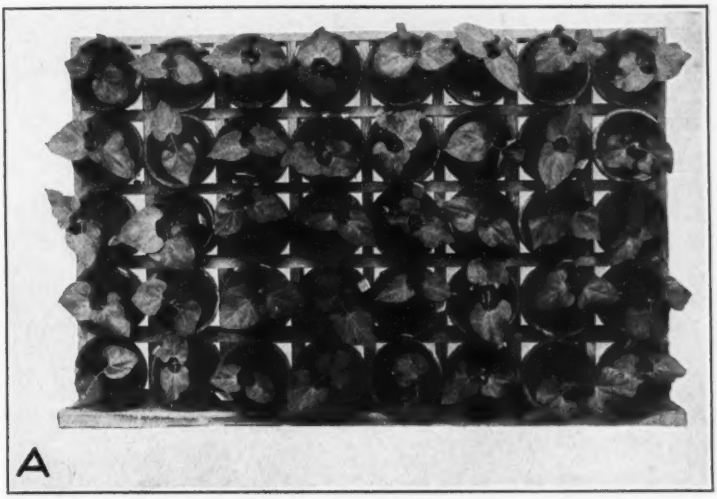
PLATE 69

A.—The frame used in the inoculation of bean plants in the greenhouse, filled with plants in position for atomization.

B.—Disks of leaves of varieties of beans photographed after extraction of chlorophyll, showing variation in response to rust inoculation in the greenhouse. All inoculated at the same time and incubated under similar conditions. *a*, Tennessee Green Pod, large uredinia; *b*, McCaslan and *c*. Navy Pea, similar to *a; d*, Yellow Eye, small uredinia; *e*, French's Horticultural, small uredinia bordered by flecks; *f*, Tennessee Wonder, small uredinia, uredinia bordered by flecks and flecks, *g*, New Pearl, large flecks; *h*, Improved Goddard, small flecks; *i*, Horticultural Pole, neither sori nor flecks.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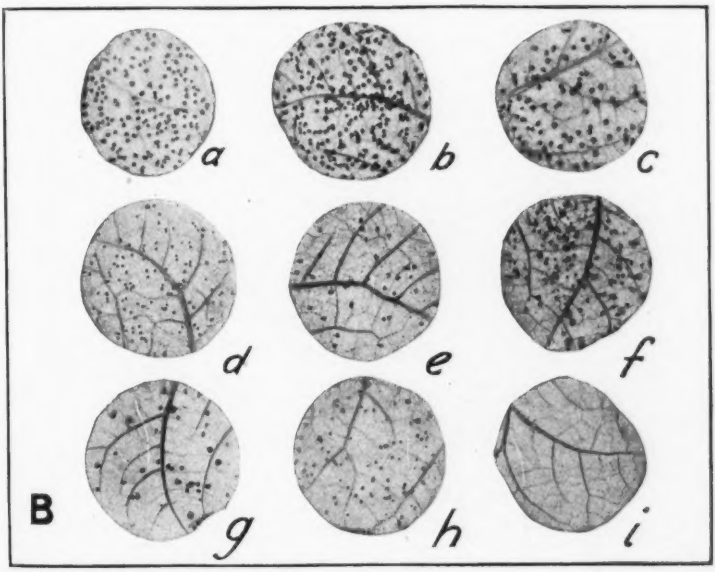
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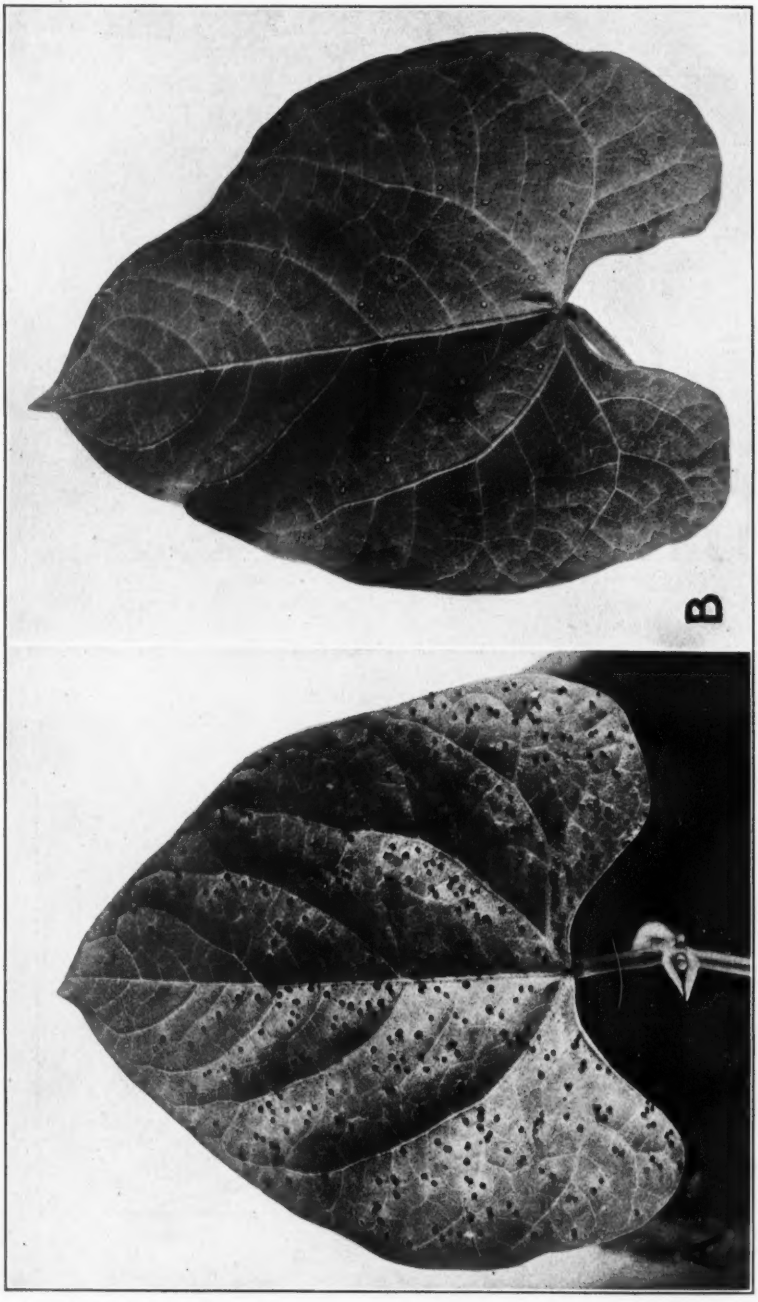
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PLATE 70

A.—Normal rust infection on a leaf of Dutch Case Knife developed in the greenhouse. Number of uredinia 544, leaf area 7.93 square inches, sori per square inch 68.6. Photographed 16 days after inoculation. Approximately natural size.

B. Abortive rust infection on a leaf of Improved Goddard. Number of flecks 140, leaf area 10.78 square inches, flecks per square inch 12.9. Photographed 16 days after inoculation. Approximately natural size.

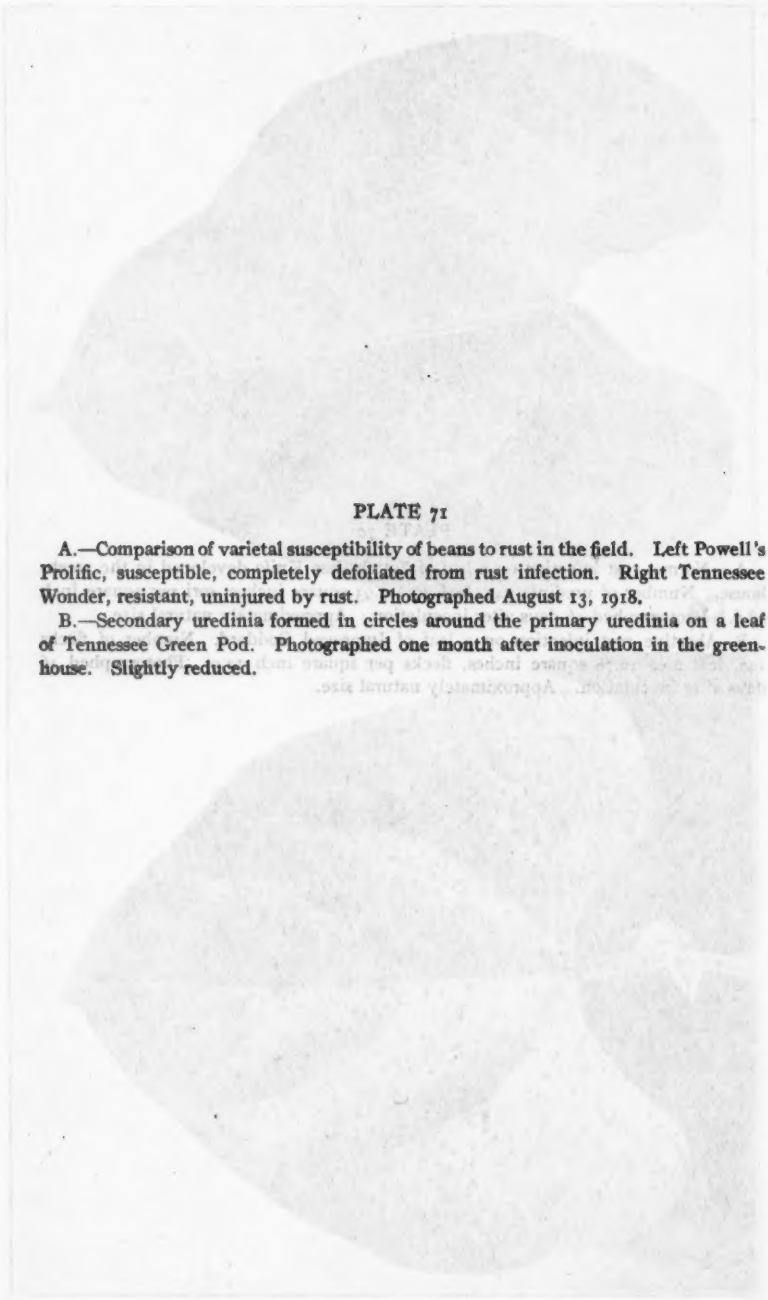
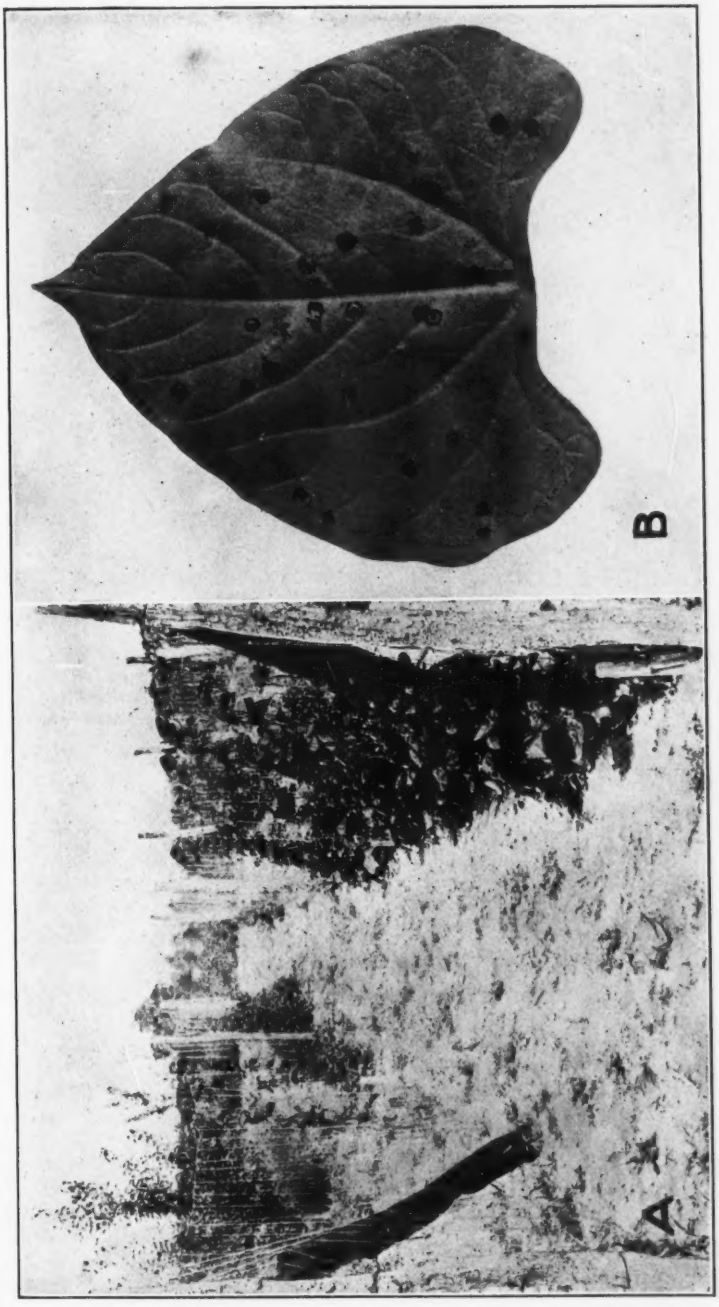


PLATE 71

A.—Comparison of varietal susceptibility of beans to rust in the field. Left Powell's Prolific, susceptible, completely defoliated from rust infection. Right Tennessee Wonder, resistant, uninjured by rust. Photographed August 13, 1918.

B.—Secondary uredinia formed in circles around the primary uredinia on a leaf of Tennessee Green Pod. Photographed one month after inoculation in the greenhouse. Slightly reduced.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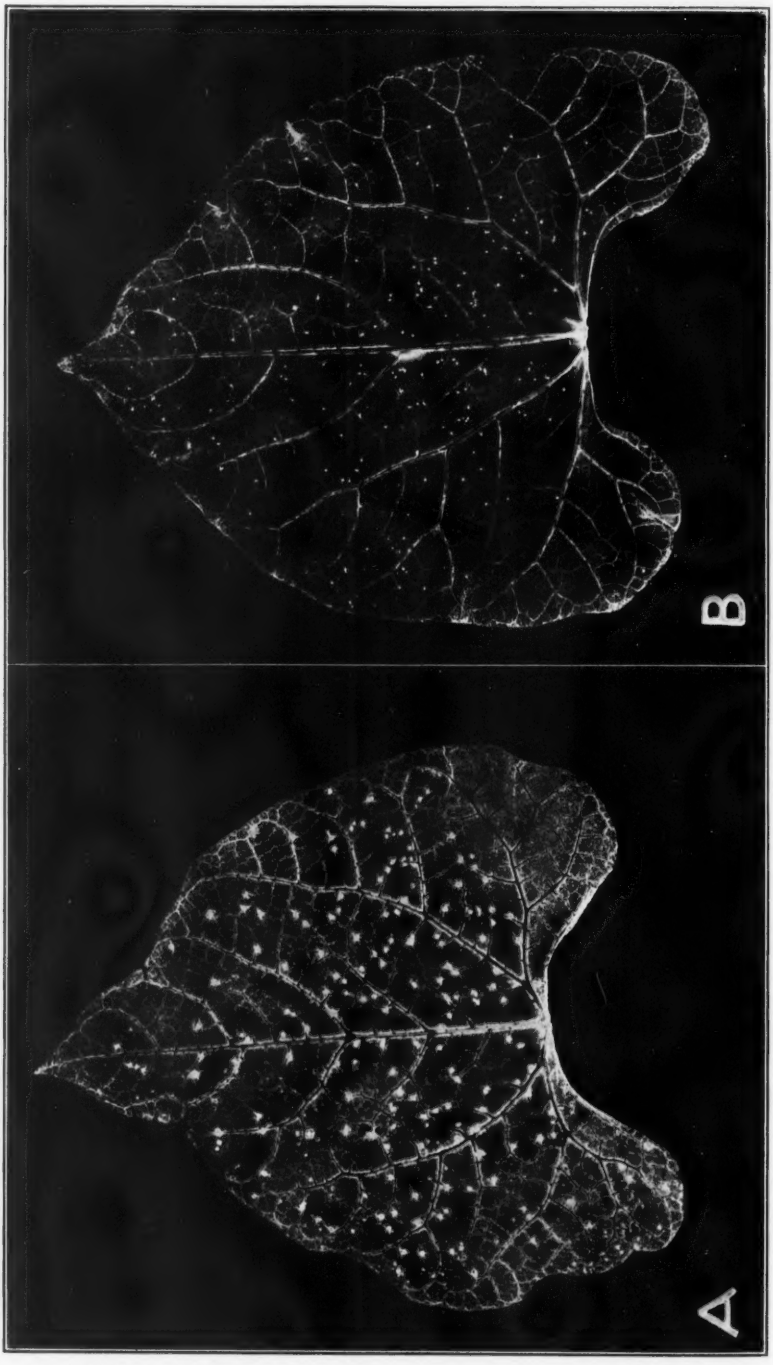
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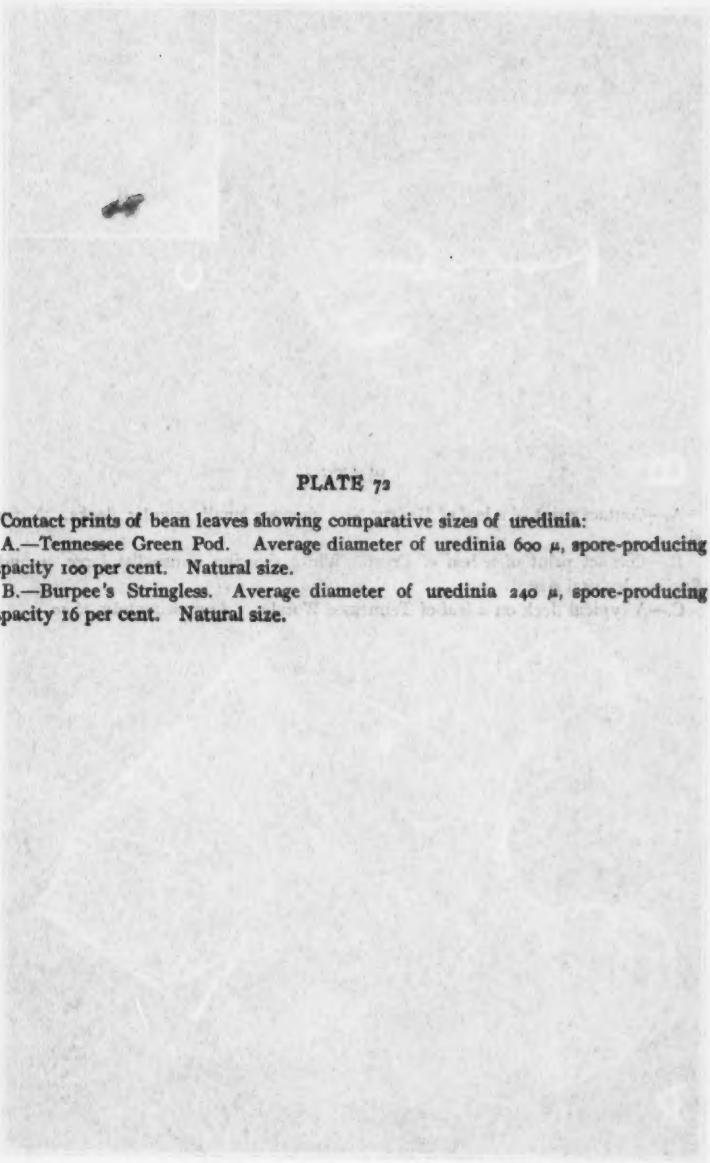


PLATE 72

Contact prints of bean leaves showing comparative sizes of uredinia:

A.—Tennessee Green Pod. Average diameter of uredinia 600 μ, spore-producing capacity 100 per cent. Natural size.

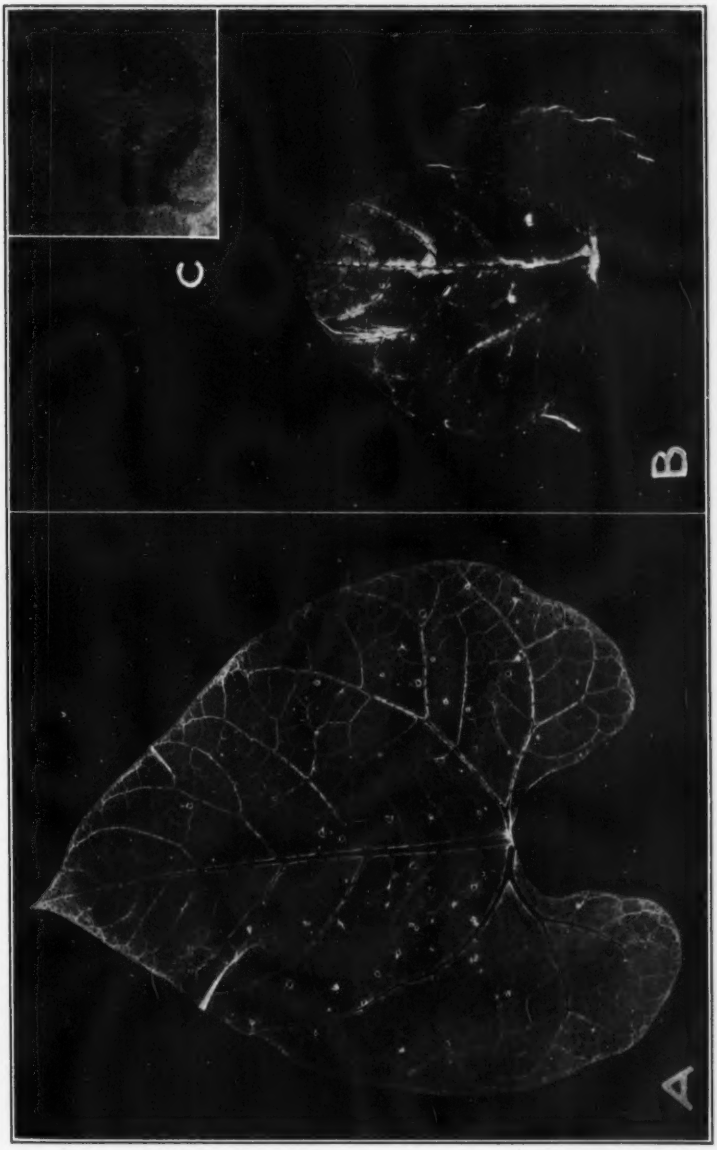
B.—Burpee's Stringless. Average diameter of uredinia 240 μ, spore-producing capacity 16 per cent. Natural size.

PLATE 73

A.—Contact print of a leaf of Mighty Nice showing small, angular flecks. Natural size.

B.—Contact print of a leaf of Crystal White showing unusually large, rounded flecks. Natural size.

C.—A typical fleck on a leaf of Tennessee Wonder. Approximately × 20.


C
B
A

LIFE-HISTORY STUDIES OF THREE JOINTWORM PARASITES

By W. J. PHILLIPS and F. W. POOS, *Entomological Assistants, Cereal and Forage Insect Investigations, Bureau of Entomology, United States Department of Agriculture*

INTRODUCTION[1]

The importance of the control of the jointworm (*Harmolita tritici* Fitch) by its parasites can not easily be overestimated. Up to the present time parasites have been the only means of control, and when these natural agencies fail whole fields of wheat often are destroyed. It is the opinion of the writers that effective control measures would have been put into practice or wheat growing in the Eastern States abandoned years ago had not the parasites of the jointworm in a large measure taken care of the situation.

The present system of crop rotation in the wheat-growing districts of the Eastern States furnishes ideal breeding grounds for the jointworm. This, however, is also true for the parasites; but we have learned by experience that we can not rely entirely upon the parasitic enemies of the jointworm to effect its control. It has been the common belief among scientists that the parasites check severe outbreaks of this pest within a few years, but the writers after studying closely a severe outbreak of the jointworm in Fauquier County, Va., have come to the conclusion that this is not always true. In that locality infestation by the jointworm has been very intense for several years, and according to observations of the past few seasons the numerical ratio of parasites to the jointworm has increased very slowly, until at the close of the year 1919 the jointworm is 92.6 per cent parasitized.

This paper treats of the life histories of three of the more important parasites of the jointworm. They are all hymenopterous parasites of the superfamily Chalcidoidea and have been mentioned frequently in literature, though no detailed accounts of their life histories as parasites of the jointworm have ever been recorded.

DISTRIBUTION

Ditropinotus aureoviridis Crawford and *Homoporus chalcidiphagus* Walsh and Riley are primary parasites, while *Eupelmus allynii* French was found to be both primary and secondary. The distribution of *D. aureoviridis* and *H. chalcidiphagus* is similar to that of the jointworm (fig. 1). *E. allynii* is commonly found wherever the Hessian fly

[1] The observations on which this paper is based were made at the United States Entomological Laboratory at Charlottesville, Va., during 1917, 1918, and 1919.

Journal of Agricultural Research, Washington, D. C. Vol. XXI, No. 6 June 15, 1921 Key No. K-96

(*Phytophaga destructor* Say) and the majority of the species of Harmolita are found. This includes practically all the wheat-growing regions of the United States. The writers feel that scientists in the past have given undue prominence to *E. allynii* as a primary parasite of the jointworm. *D. aureoviridis*, where it is normally found, occurs in greater abundance than either of the other two parasites treated in this paper.

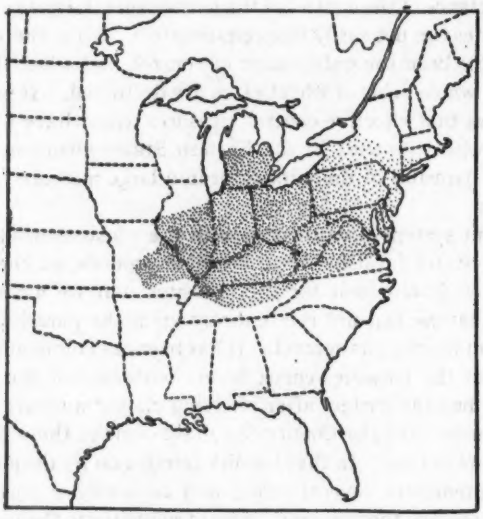


FIG. 1.—Present known distribution of the wheat jointworm in the United States.

METHODS OF REARING

The adult parasites used in this breeding work were obtained from material collected in various localities and kept through the winter at the laboratory at Charlottesville, Va., under as nearly normal conditions as could be provided. The parasites were placed in a cage (Pl. 79, A) which contained stock material of *Harmolita tritici*. This cage was a glass cylinder 9 by 14 inches, having a cheesecloth cover. It was placed upon a saucer of moist sand into which the stems containing galls of *H. tritici* were placed. The ordinary greenhouse wooden label was used for identification of the cages. Another very successful breeding cage (Pl. 74, A) which was used consisted of a lantern globe with a cheesecloth cover, placed upon a 5-inch pot. The parasites were given fresh straws for oviposition each morning and a few drops of dilute sugar water for them to feed upon. Feeding once a day seemed sufficient to supply the needs of the parasites. Oviposition was observed in these cages, and the stems were removed promptly and dissected. Eggs with their host were removed to glass cell cages [1] which were made for this

[1] PACKARD, C. M. LIFE HISTORIES AND METHODS OF REARING HESSIAN FLY PARASITES. *In* Jour. Agr. Research, v. 6, no. 10, p. 367–382, pl. 51–52. 1916.

purpose (Pl. 74, B). This cage was made by cutting window glass to the size of ordinary glass slides, and by the use of a dentist's small burr or carborundum grinder making a single small cell large enough to accommodate the larva of *H. tritici* in one surface of each slide. After a single egg with its host had been placed in each cell, the cell was closed with the ordinary glass cover slip, to which was applied a droplet of honey to hold it in place. The usual label was pasted on each slide for identification, and the slides were then placed in small closed pasteboard boxes in order to exclude the light. The life stages of the parasites from egg to adult could thus be observed under the microscope. Often, however, the parasite larva would crawl away from its host and starve during the night. Sometimes the host larva would turn dark as if decaying and another would have to be substituted. After long experience and with all possible care that could be given, it was found impossible to rear more than about 60 per cent of a given number of parasites by the cell-slide method. But since this method was the only one known in which the different stages could be observed continuously, it was adhered to throughout. *Eupelmus allynii* bred very freely by this method, while *Homoporus chalcidiphagus* bred less freely and *Ditropinotus aureoviridis* with some difficulty. The larvæ of the last-named species completed their development very readily, but very few continued through to the adult stage.

In order to have a control on the period of development of the parasites in the cell slides (Pl. 79, B), some of the eggs of the same age were not removed from the Harmolita cells but were permitted to remain and develop normally as they would in the field. It was found that each of these species very closely approximated the same period of development when reared in the glass cell as when reared in the galls of the jointworm under the same weather conditions.

In observing the larval development of these parasites it was comparatively easy to identify the various instars of *Ditropinotus aureoviridis* and *Eupelmus allynii* by the length, number, and position of the setæ and the change in size and shape of the larvæ. The instars were verified by making a balsam mount of each cast skin. It was found impossible to identify all of the instars of *Homoporus chalcidiphagus* except by removing to a balsam mount the entire contents of a glass cell, where the individual larva had developed, and noting the number of pairs of mandibles remaining therein.

All observations indicate that only one specimen of any of the three species studied ever matures in a single Harmolita cell. An individual host larva seems to furnish just enough food for a single parasite. Usually only the old dried skin of the host remains after the parasite larva has become full grown.

DITROPINOTUS AUREOVIRIDIS[1]

This species was first described, both male (fig. 2) and female (fig. 3), by Mr. J. C. Crawford in 1907.[2] In 1912, Mr. A. B. Gahan[3] described

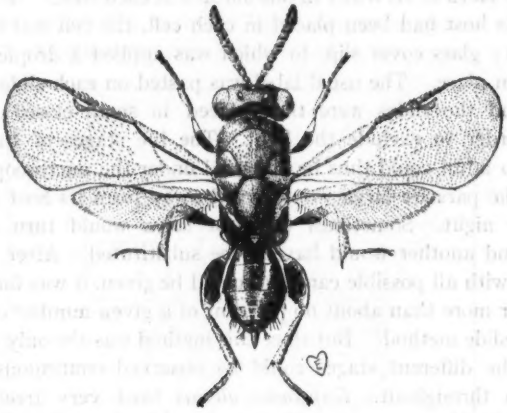


FIG. 2.—*Ditropinotus aureoviridis:* Adult male. Greatly enlarged.

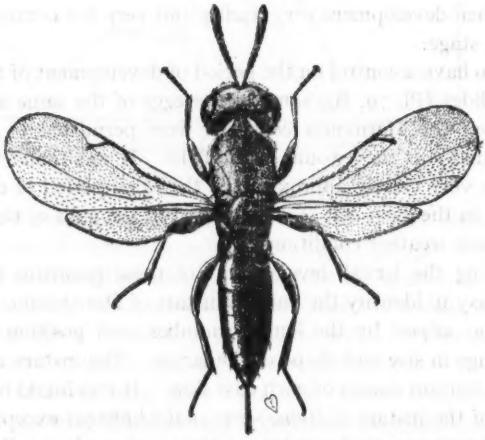


FIG. 3.—*Ditropinotus aureoviridis:* Adult female. Greatly enlarged.

the species *Ditropinotus flavicoxus*, basing his species on the very light coloration of the coxæ. Since publishing this description Mr. Gahan thinks it possible that *D. flavicoxus* may be only a varietal form of *D. aureoviridis*. The present writers have never reared a typical specimen

[1] Family Torymidae, Subfamily Monodontomerinae.

[2] CRAWFORD, J. C. NEW NORTH AMERICAN HYMENOPTERA. *In* Jour. N. Y. Ent. Soc., v. 15, no. 4, p. 178–179. 1907.

[3] GAHAN, A. B. DESCRIPTIONS OF TWO NEW GENERA AND SIX NEW SPECIES OF PARASITIC HYMENOPTERA. *In* Proc. Ent. Soc. Wash., v. 14, no. 1, p. 5–6. 1912.

of *D. flavicoxus*, though some specimens reared have much lighter-colored coxæ than those of the average *D. aureoviridis*.

HOSTS

This species apparently prefers *Harmolita tritici* and *H. vaginicola* Doane, and the writers have reared it in cell slides on *H. elymicola* Phillips and Emery and *H. grandis* Riley. It probably will parasitize any of the gall-forming species of Harmolita, though the writers have reared it only from field collections of *H. tritici*, *H. vaginicola*, *H. grandis*, *H. atlantica* Phillips and Emery, and *H. secalis* Fitch. It breeds freely upon the larvæ of *Eurytoma* spp. in the field and in breeding cages, and upon one occasion an egg was deposited in a Harmolita cell upon a pupa of *Ditropinotus aureoviridis*. It undoubtedly breeds upon *Homoporus chalcidiphagus* also, though it plays the rôle of secondary parasite only when the individuals of Harmolita are very highly parasitized.

EGG

The eggs (Pl. 75, A; 77, B) are deposited in the gall-like cells of *Harmolita tritici* external to the host larva. They are not always placed directly upon the host, but the small size of the cell of the jointworm requires that the egg be in close proximity to its host. The egg is grayish white in color and opaque. It is elongate, kidney-shaped, but asymmetrical. There is a nipple-like process at each end of the egg. The surface of the egg is covered uniformly with spicules with the exception of the nipple-like process at the posterior end. The average of four eggs measured 0.6772 mm. in length and 0.1583 mm. in greatest width.

The period of incubation of 199 eggs in cell slides varied at different times during the breeding season from 1 to 5.5 days. The average time was 3 days. Low temperatures greatly retarded development. At the time the egg is ready to hatch, the mandibles of the young larva can be observed at the large end of the egg, where they move back and forth occasionally. Sometimes the whole outline of the head can be seen through the chorion just before the young larva cuts its way out with its mandibles. The round nipple-like process extended out beyond the larva's head makes it look as though it were wearing a dunce cap. The larva keeps pushing forward with its head against the flexible shell, at the same time slashing away with its mandibles until finally the shell is ruptured. The larva then forces its head through the aperture (Pl. 75, B) and begins feeding at once upon the host larva. Several hours are usually required for the larva to extricate itself from the eggshell.

LARVA

FIRST INSTAR (Pl. 75, C).—The color of the first-instar larva is translucent whitish. Just before the first molt the average length of three larvæ was 0.9152 mm. and the average greatest width was 0.2060 mm.

When hatched the larva is very slender and gradually tapers toward the posterior extremity. At this time the head (Pl. 75, D) is considerably larger than the individual body segments. Just before the first molt is cast (Pl. 75, E) the head is much narrower than any of the first 8 body segments. The head is convex anteriorly and bears 7 pairs of rather long setæ and a pair of fleshy cylindrical tubercles which apparently are antennæ. The mandibles of this stage (Pl. 76, A) appear to be very highly chitinized, very slender and pointed. The body consists of the usual 13 segments bearing 5 pairs of spiracles, a pair on each of the last 2 thoracic and first 3 abdominal segments. There are 2 lateral rows and 2 subdorsal rows of long setæ, 1 seta to each row to each body segment, and 2 subventral rows of long setæ on the thoracic segments only; in addition, around each segment there are 2 or more irregular rows of minute setæ.

SECOND INSTAR (Pl. 75, F).—Color as in previous instar. Average length of three larvæ 1.1645 mm. and average greatest width 0.3473 mm. In this instar the larva is pointed at each extremity although very much more pointed posteriorly. The head is convex anteriorly and bears 5 pairs of setæ; antennæ as in previous instar. The mandibles (Pl. 76, B) have changed shape entirely; they are very broad at the base and much less heavily chitinized than in the previous instar. There are 9 pairs of spiracles present, 1 pair to each of the last 2 thoracic and first 7 abdominal segments. The short, minute setæ present in the first instar are not present in this or any of the succeeding instars, and the long setæ are shorter but are arranged on the body as in the previous instar.

THIRD INSTAR (Pl. 75, G).—Color same as in previous instar; average length of three larvæ 1.3533 mm. and average greatest width 0.4083 mm. Shape is much the same as in the previous instar. Head bears 8 pairs of setæ, which are longer than in the previous instar; antennæ same; mandibles (Pl. 76, C) much longer and more slender and about as heavily chitinized as in the previous instar. The setæ of the body are much more numerous and are longer than in the previous instar. The first segment bears a partial double row of setæ around it; the other segments bear an irregular single row of setæ of unequal length around them.

FOURTH INSTAR (Pl. 75, H).—Color and shape as in previous instar; average length of three larvæ 2.1233 mm. and average greatest width 0.5833 mm. Head as in previous instar except that setæ have become much longer and more numerous; antennæ same; mandibles (Pl. 76, D) same general shape as in previous instar, but larger. The setæ of the body are more numerous and are longer than in the previous instar, There are three incomplete, irregular rows of setæ around the first thoracic segment; two rather complete, irregular rows around the second; an irregular single row around the last thoracic and all the abdominal seg-

ments with the exception of the ninth, which bears a partial double row irregularly placed. Setæ are of uneven length as in previous instar

FULL-GROWN LARVA (fig. 4).—Color: Larva has a slight ferruginous tinge, due to the setæ; the body is dirty whitish with a dark central area, due to the contents of the digestive tract; the average length of 5 larvæ was 3.108 mm., and the greatest width averaged 1.106 mm. In this stage the larva is less pointed, broader, and thicker and much more hairy than at any previous stage; setæ cover the entire surface of the head except for a narrow line down the center of the face; there also seems to be a slightly chitinized area down the face on each side of this median line. Antennæ apparently the same as in previous instars. Mouthparts (Pl. 76, F): Mandibles (Pl. 76, E) same as in previous instar with the exception that they are considerably larger. Labrum consists of a simple triangular piece and is only very slightly chitinized; maxillæ and labium exist only as fleshy lobes slightly chitinized on their surface

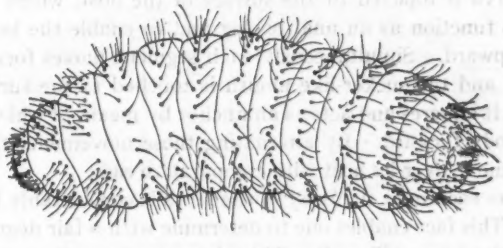


FIG. 4.—*Diltropinotus aureoviridis:* Full-grown larva. × 24.5.

and bear 8 setæ and 4 groups of slight elevations or tubercles. (See Pl. 76, F.)

The setæ of the body are longer and much more numerous than in the previous instar; each segment except the last four abdominal bears an irregular row of very long setæ around it; in addition, the first thoracic segment bears a second irregular row of varying length around it; the second thoracic segment bears a second row likewise and a partial third around it; the third thoracic segment bears only one additional row around it; the first abdominal segment bears a partial second row; the second, third, fourth, fifth, and sixth the same. The seventh, eighth, and ninth bear numerous setæ, varying greatly in length, that can scarcely be designated as constituting definite rows; the last segment bears numerous small setæ and is invaginated laterally.

In order that the number of larval instars might be ascertained, the larvæ were kept under almost constant observation under the microscope night and day from the time they were hatched until they became full-grown. By this method there appeared to be four fairly distinct larval molts, as indicated by the external changes of the larvæ. These observations were verified by making balsam mounts of the cast skins of

the individual larvæ and noting the number of pairs of mandibles. Five pairs of mandibles, gradually increasing in size (Pl. 76, A–E), were thus found, seeming to give definite proof of the accuracy of the observations.

As soon as the young larva hatches, it pushes its head out of the egg-shell (Pl. 75, B) and immediately begins to feed. It often feeds thus for about 24 hours before it completely extricates itself from the shell. In this stage it often feeds with only its head touching the host. It apparently slashes away with its mandibles until it has made a slight incision in the body wall of the host, whereupon it begins to suck up the body fluids. The larva feeds almost continuously, if undisturbed, until nothing remains of the host larva but the empty skin. When the parasites are very abundant, very often several eggs are found in a single jointworm cell, but never more than one larva completes its development therein. The largest and strongest larva evidently overcomes and destroys the others. In moving forward over its host the tip of the abdomen of the parasitic larva is touched to the surface of the host, where it adheres. It seems to function as an anal proleg and to enable the larva to bow the body upward. Simultaneously each segment moves forward as far as possible, and the sucker-like mouth is touched to the surface of the host, where it adheres and acts as an anchor by means of which the larva pulls the body forward. By alternating these movements the larva is enabled to move over its host with comparative ease.

Just before each molt the body of the larva is considerably larger than the head. This fact enables one to determine with a fair degree of accuracy when the larva will molt. This character is much more apparent in the early stages. The later stages are indicated more clearly by the increased number of setæ. The duration of instars, as is common with most insects, varies with the temperature, hot weather accelerating and cooler weather retarding development. The first instar lasts from one to four days; later instars approximate this period of time, varying directly with temperature and the condition of the host.

Larvæ of this species which were reared in glass cells became full-grown in from 6 to 24 days. One hundred and thirty-seven larvæ observed for this purpose at various times during the breeding season became full-grown within an average of 11 days.

During the season of 1917, 41 larvæ became full-grown in glass cells, but died during the winter before any of them pupated. In 1918, out of more than 100 larvæ, which became full-grown in glass cells, only 9 pupated during the same season. Those that pupated did so within a period of from 4 to 17 days after they had completed feeding. These individuals were of the first and second generations. Sixteen adults emerged from the remaining material, and several others pupated. Both first- and second-generation larvæ completed development the following spring. Five of this group were kept in the laboratory, and the remaining larvæ were kept in a cellar during the winter. Cage material

reared in Harmolita galls as a control on those reared in glass cells for the purpose of determining how well the glass cells approximated normal conditions for these parasites, for that particular season, showed that many larvæ of the first generation did not pupate during that season. This was found to be true likewise of *Homoporus chalcidiphagus*.

PREPUPA

The prepupal stage (Pl. 77, A; fig. 5) in three specimens observed varied from 1 to 6 days, with an average of 2 days. The larva does not void excrement during its earlier stages of development, but when the full-grown larva is ready to pupate, a considerable amount of excrement is voided and the specimen contracts considerably. The first four segments of the abdomen contract equally until each is somewhat less than half its usual length in the full-grown larva. If the specimen is viewed from the ventral aspect, the last two segments of the abdomen appear

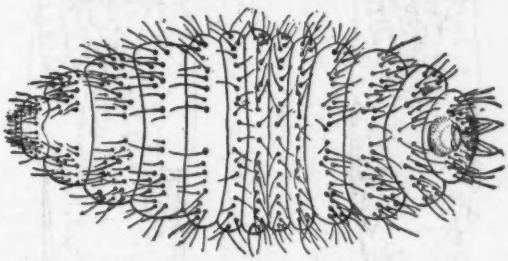


FIG. 5.—*Ditropinotus aureoviridis:* Prepupal stage. × 34.

to curve backward dorsally. The measurements of two prepupæ averaged 2.2050 mm. in length and 0.9450 mm. in greatest width.

PUPA

Pupation was observed upon one occasion, the process requiring 17 minutes. The fully developed pupa was plainly visible through the old larval skin, which first split down the center of the head, and the pupa then gradually worked itself forward through the opening. At first the pupa is a very delicate brown in color, gradually changing and becoming very dark, approximating the color of the adult insect. The pupal stage varies in length from 8 to 15 days. The average for 8 specimens observed in glass cells was 10 days. Six female pupæ (Pl. 77, C; fig. 6) averaged 3.0479 mm. in length and 0.8108 mm. in greatest width. One male pupa (Pl. 77, D; fig. 7) measured 2.66 mm. in length and 0.91 mm. in greatest width.

ADULT

No males normally occur in the first generation of this species, and the females seem greatly to outnumber the males in succeeding generations. They pass the winter as full-grown larvæ in the gall-like cells

of the jointworm, and the first generation of this parasite begins to emerge about the first week in June and the second generation about the first week in July in Virginia, according to the authors' records. Previous to the season of 1918 it was supposed that there were only two generations each year; but during 1918 and 1919 two complete and a partial third generation were reared in glass cell slides,[1] and apparently a partial third one was reared from the field in 1919. There appeared to be only two main generations annually in the field, and further observations, therefore, are necessary before it can be determined definitely whether there is normally a partial third generation under field conditions.

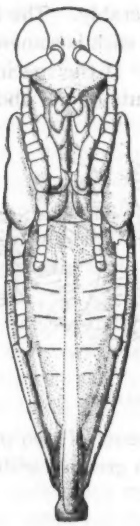


FIG. 6.—*Ditropinotus aureoviridis:* Pupa of female. × 25.

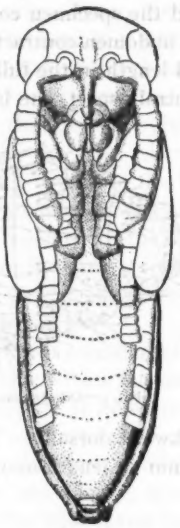


FIG. 7.—*Ditropinotus aureoviridis:* Pupa of male. × 28.

The largest number of eggs secured from a single female was 18 during a period of 12 days. One female lived 48 days. When the female is ready to oviposit she walks up and down the wheat stem, tapping it with her antennæ until a jointworm gall is located. After locating a suitable cell the female brings the abdomen almost at right angles to the thorax, at the same time elevating the body as much as possible. She then touches the tip of the ovipositor to the surface of the wheat stem. In this position she uses her ovipositor very much as a gimlet until it is forced into the Harmolita cell, at which time the body assumes its more nearly normal position. The egg, after oviposition, has the same shape as before oviposition. Five to 10 minutes are required for the female

[1] This observation was repeated in 1920 with the same results.

to deposit one egg. The females have been observed ovipositing at night in the breeding cages, but the greatest activity occurs during daylight.

HOMOPORUS CHALCIDIPHAGUS[1]

This species was first described, male and female (fig. 8), in 1869.[2] This is one of the oldest recorded parasites of the jointworm and has been reported many times in literature, though the detailed account of its life history has not as yet appeared in print.

Next to *Ditropinotus aureoviridis* it is the most important parasite of *Harmolita tritici* in Michigan, Illinois, Indiana, Ohio, Kentucky, Tennessee, and Missouri. In the Atlantic States *Eurytoma* sp. is probably of greater importance than *H. chalcidiphagus;* in fact, at some points *Eurytoma* spp. undoubtedly ranks first in importance of the parasites of *H. tritici*. *H. chalcidiphagus* undoubtedly suffers more from the depredations of secondary parasites than any of the other primary parasites of the jointworm that have come under the observation of the writers. As evidence of this fact, *H. chalcidiphagus* was very abundant at Warrenton, Va., when the status of the various parasites was first studied there, whereas at the present time it scarcely exists in this locality. This is true in spite of the fact that there are five generations a year of

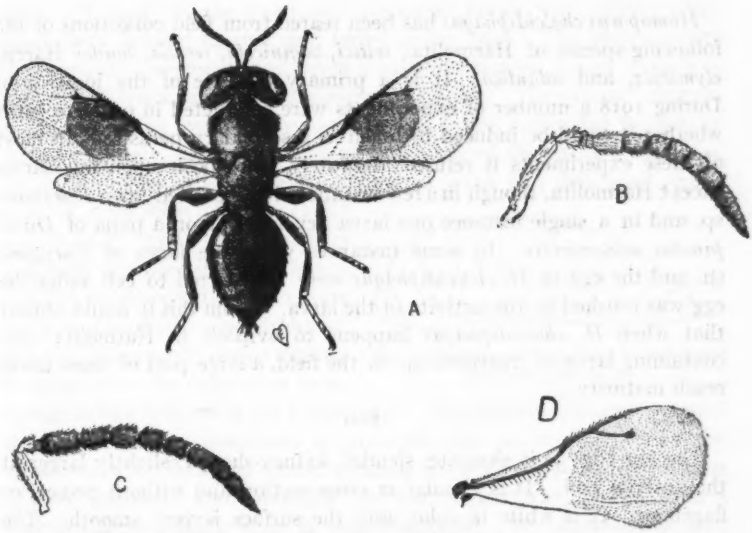


FIG. 8.—*Homoporus chalcidiphagus:* A, Adult female; B, antenna of adult female; C, antenna of adult male; D, wing of adult male.

[1] Family Pteromalidae, Subfamily Merisinae.

[2] WALSH, Benjamin D., and RILEY, Charles V. THE JOINT-WORM (ISOSOMA HORDEI HARRIS). *In* Amer. Entomologist, v. 1, no. 8, p. 152. 1869.

this parasite in the vicinity of Charlottesville. *Eupelmus allynii* is undoubtedly largely responsible for this condition of affairs, although *D. aureoviridis* very probably assists greatly in bringing about the condition which has been noted above. The larvæ of *H. chalcidiphagus* are very smooth and inactive and apparently are as easy prey to other parasites as are the Harmolita larvæ. *Eupelmus allynii* and *D. aureoviridis*, on the contrary, are very active and therefore can defend themselves to a large extent. This is particularly true of *D. aureoviridis*, which is very hairy and very active and usually can crush the egg of other parasites before hatching is possible.

HOSTS

Homoporus chalcidiphagus has been reared from field collections of the following species of Harmolita: *tritici*, *vaginicola*, *secalis*, *hordei* Harris, *elymicola*, and *atlantica*. It is a primary parasite of the jointworm. During 1918 a number of experiments were conducted in order to learn whether it could be induced to breed as a secondary parasite. In most of these experiments it refused absolutely to oviposit upon any larvæ except Harmolita, though in a few instances it oviposited upon *Eurytoma* sp. and in a single instance one larva developed upon a pupa of *Ditropinotus aureoviridis*. In some instances when the larva of *Eurytoma* sp. and the egg of *H. chalcidiphagus* were transferred to cell slides the egg was crushed by the activity of the larva. From this it would appear that when *H. chalcidiphagus* happens to oviposit in Harmolita cells containing larvæ of *Eurytoma* sp. in the field, a large part of these never reach maturity.

EGG

The egg (fig. 9) is elongate, slender, kidney-shaped, slightly larger at the anterior end. It is circular in cross section and without pedicel or flagellum. It is white in color, and the surface is very smooth. The average length of 4 eggs was 0.4204 mm. and the greatest width 0.1347 mm. They are always found external to the host. Sometimes as many as 4 or 5 were found in one cell of *Harmolita tritici*, but never more than one larva completed its development when more than one egg was placed upon a single host. Some of the eggs for some cause or other shriveled up and failed to hatch. This was not due to handling, since the eggs were found to be shriveled when the jointworm cells were opened. In hatching, the larva ruptures the large end of the egg and begins feeding before it completely emerges from the shell. The period of incubation in glass cells varied from 1 to 4½ days, depending upon weather conditions, warm weather accelerating and cool weather retarding development. The average length of the egg stage of 71 eggs observed was about 2.5 days.

FIG. 9.—*Homoporus chalcidiphagus*: Eggs. × 47.5.

LARVA

FIRST INSTAR (fig. 10).—Newly hatched larvæ are translucent whitish in color; the average length of three larvæ in this stage was 0.3945 mm. and the greatest width, 0.1490 mm. When hatched the larva tapers toward each extremity but is pointed posteriorly; it is very smooth, the setæ being so small that it is practically impossible to determine the exact number. There is a pair of prominent fleshy elevations or tubercles on the front of the head that are apparently the antennæ. The head is very smooth, and if any setæ are present they are so small that it is almost impossible to ascertain their number and position. The mandibles (Pl. 76, G) of the first instar are simple hooks, very slightly chitinized, very pointed at tips, and broad at the base. The body consists of the usual 13 segments and bears 5 pairs of spiracles, a pair to each of the last 2 thoracic and first 3 abdominal segments. The external changes in the succeeding instars were so slight that it was impossible to identify them accurately. A balsam mount was made of the entire contents of one of the glass cells where an individual larva had developed and 5 pairs of mandibles (Pl. 76, G–K) were found. As all of these pairs gradually increased in size it is reasonable to suppose that they were those of *Homoporus chalcidiphagus*. One pair (the fourth) differs slightly in shape from the other four pairs, though in size it fits in as the fourth pair. The slightly different shape of the fourth pair of mandibles is probably due to the fact that the mandibles are difficult to mount so as to have all the pairs in the same relative position, and probably the fourth pair was viewed from a slightly different angle when it was illustrated. No illustrations other than those of the mandibles were made of any of the larval instars, except the first and the full-grown larvæ, since none of the other instars could be determined accurately.

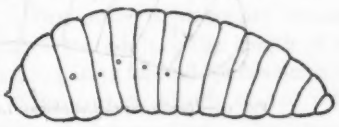


FIG. 10.—*Homoporus chalcidiphagus:* Lateral view of first-instar larva. × 128.

FULL-GROWN LARVA (Pl. 74, D; fig. 11).—Color dirty whitish, with a dark line showing through the center of the larva due to the contents of the digestive tract. The average length of five full-grown larvæ was 3.08 mm., and the greatest width was 0.91 mm. The full-grown larva is of the same general shape as the first-instar larva. The last abdominal segment is clearly invaginated laterally. The head (Pl. 76, M) is very smooth and bears a pair of rather prominent fleshy elevations or tubercles on the front that are evidently the antennæ. It also bears four pairs of very small setæ—one pair laterad of the mandibles; a pair laterad of these, about the middle of the cheek; a pair dorsad of these; and a fourth pair above and inside the antennal region. There are three pairs of minute

setæ just above the labrum. Mouthparts (Pl. 76, L) and mandibles (Pl. 76, K) are the same general shape as in the first instar, though much larger and somewhat more heavily chitinized. The labrum is a small fleshy triangular piece. The labium and maxillæ are fused and exist only as fleshy lobes bearing three pairs of minute setæ and four pairs of very slight elevations or tubercles.

The body bears 9 pairs of spiracles, a pair to each of the last 2 thoracic and first 7 abdominal segments; the setæ are so small that it is almost impossible to locate them definitely, although there are apparently 4 rows on the ventral surface of the 3 thoracic segments, 2 lateral rows, and 2 subdorsal rows extending the entire length of the body, 1 seta on each segment in each row, with the exception of the last abdominal segment which bears 2 pairs of subdorsal setæ. As indicated previously, the 5 pairs of mandibles found in the cell slide where an individual of

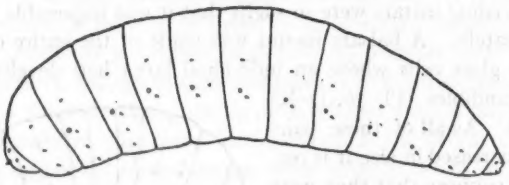


FIG. 11.—*Homoporus chalcidiphagus:* Lateral view of full-grown larva. × 24.7.

this species had pupated indicate that there are four larval molts during the development of this species.

The feeding habits of this larva are very much the same as those of *Ditropinotus aureoviridis*, though the larvæ are very much more delicate and less active; consequently, they are more difficult to rear to full-grown larvæ. Observations on 42 larvæ of this species showed that they became full-grown in glass cells in from 5 to 25 days, depending upon weather conditions and the condition of the host. During the summer they developed very rapidly, while in the fall the period was greatly lengthened. The average period of development was about 11 days. The average period of time between the full-grown larva and the prepupal stage for 40 individuals was 4½ days. In a large number of cases the larvæ became full-grown and remained quiescent for many months. Many then contracted slowly and died, while others completed their development to adults the following season. In one instance 2 larvæ remained in the quiescent stage from August, 1917, until September, 1918, when they finally died. At the present time, December, 1919, the writers have living larvæ in the quiescent stage which became full-grown larvæ as early as June, 1918. The winter is passed as full-grown larvæ in the cells of the jointworm.

PREPUPA

The prepupal stage (Pl. 74, C; fig. 12) of the larva is indicated by the contraction of the anterior abdominal region, the greatest constriction occurring in the first 2 abdominal segments which contract to about one-half the original width. In this stage a large amount of excrement is voided and the prepupa is then pure white in color. No excrement is voided during any period of larval growth. Observations on 37 individuals showed that they remained in this stage from 1 to 6 days, the average being about 2 days. The average length of three prepupæ was 2.4966 mm. and the greatest width averaged 0.8633 mm.

FIG. 12.—*Homoporus chalcidiphagus*: Ventral view of prepupa. × 20.

PUPA

The pupa (Pl. 74, E–G) of this species is at first pure white. The eyes first begin to turn pink and gradually grow darker as the remaining portions of the body become dark. The entire pupa finally becomes bluish black, approximating the color of the adult. The length of the pupa stage was found to vary from 5 to 23 days for individuals pupating during the same breeding season. The average length of the pupal period for 64 individuals was between 9 and 10 days. The average length of 3 female pupæ was 3.5 mm. and the greatest width averaged 0.7933 mm.; the average length for 3 male pupæ was 2.7533 mm.; and the greatest width averaged 0.7933 mm. The male pupa can easily be distinguished from the female pupa by the fact that the antennæ extend the full length of the tarsi of the forelegs. This is not true of the female pupa.

ADULT

The adult (fig. 8) emerges in Virginia during the latter part of May and continues breeding up into the month of October. Even in the northern States on warm days in October this parasite has been observed in the fields. Five complete generations were reared at this laboratory in cell slides from May to September in 1918. These observations accorded with rearings in Harmolita galls in wheat stems kept under similar conditions.

Males normally occur in about equal numbers with females, though this species will breed parthenogenetically, in which case the offspring are males.

The average number of eggs deposited for 5 individual females was 31.8, for an average period of 15.2 days. One individual deposited 45 eggs during a period of 17 days. One individual lived for 31 days. The

females always took up a position with the head directly up the stem in ovipositing. The process of oviposition was very much the same as described for *Ditropinotus aureoviridis*. The shape of the egg of *Homoporus chalcidiphagus* is the same after oviposition as before.

EUPELMUS ALLYNII[1]

This species (figs. 13, 14, 15) was first described in 1882.[2] In 1916 Mr. C. M. Packard[3] gave an excellent account of the life history as a

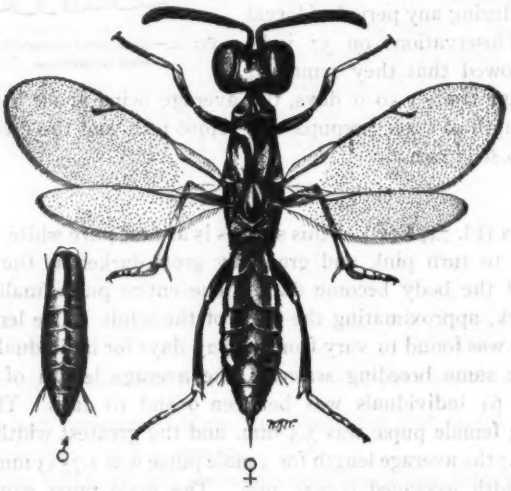


FIG. 13.—*Eupelmus allynii:* Adult female and abdomen of male, greatly enlarged. (Webster.)

parasite of the Hessian fly, and his paper is the only published record on the detailed life history of this species. It has been considered by some

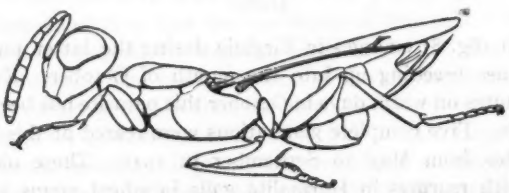


FIG. 14.—*Eupelmus allynii:* Lateral view of adult female, greatly enlarged. (Webster.)

writers as the most important parasite of the jointworm. In the estimation of the present writers it ranks about fourth in importance in the list of parasites of *Harmolita tritici*.

[1] Family Encyrtidae, Subfamily Eupelminae.

[2] FRENCH, G. H. THE WHEAT-STRAW WORM. (ISOSOMA ALLYNII, FRENCH.) *In* 11th Rpt. State Entomologist Ill. [1881], p. 73–81. 1882.

[3] PACKARD, C. M. LIFE HISTORIES AND METHODS OF REARING HESSIAN-FLY PARASITES. *In* Jour. Agr. Research, v. 6, no. 10, p. 367–382, pl. 51–52. 1916.

HOSTS

Eupelmus allynii is both a primary and a secondary parasite of the jointworm. It apparently will breed as freely as a secondary parasite in jointworm cells as upon jointworms themselves under both field and cage conditions. It has been found breeding as a secondary parasite on *Ditropinotus aureoviridis*, *Homoporus chalcidiphagus*, and *Eurytoma* sp. both in cages and in the field. We have reared it in connection with other parasites from the following species of Harmolita from field collections: *tritici*, *vaginicola*, *maculata* Howard, *elymicola*, *elymivora* Phillips and Emery, *atlantica*, *albomaculata* Ashmead, *grandis* form *grandis*, and from what is thought to be a new species which forms galls in *Panicum clandestinum* L.; also probably from *H. occidentalis* Phillips and

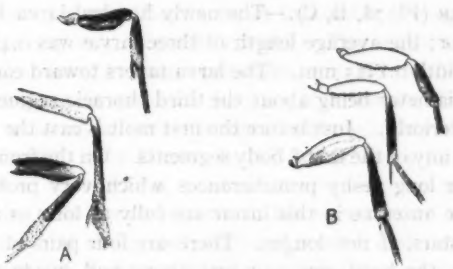


FIG. 15.—*Eupelmus allynii:* A, Legs of female; B, legs of male; greatly enlarged.

Emery, and *H. hesperus* Phillips and Emery. In the majority of these instances it can not be said positively whether or not it was breeding as a primary parasite. It may have been and probably was breeding as both a primary and a secondary parasite in each instance. It will probably breed upon any species of the genus Harmolita.

EGG

The egg (Pl. 77, E, F; 78, A) of this species is perfectly smooth without any sculpturing whatever and is white in color. The average length of four eggs was 0.4109 mm., and the greatest width 0.1578 mm. It is ellipsoidal in shape; the chorion is thin and elastic; there is a pedicel at the cephalic pole of the egg that is nearly as long as the egg itself and a slender flagellum at the opposite pole that is scarcely one-fourth as long as the pedicel. The pedicel is usually folded back against the egg after oviposition.

The egg is always deposited external to the host. About 50 per cent of the eggs found were fastened to the wall of the Harmolita cell by means of a delicate, fibrous, netlike structure which was apparently woven from fine white threads (Pl. 77, E). When this covering was found over the eggs it was usually fastened down rather firmly all around

the edges, holding the egg securely in place. As many as eight eggs have been found in one Harmolita cell, in which case there was always a separate covering for each egg, though these coverings were usually attached to each other.

The period of incubation of 79 eggs varied from 1 to 4.5 days during the breeding season, depending upon weather conditions. The average length of the incubation period for these 79 eggs was 2.4 days.

In the process of hatching it was observed that the head of the larva broke through the chorion near the base of the pedicel. The eggshell is apparently ruptured in the same manner as is that of *Ditropinotus aureoviridis*, previously described (p. 409).

LARVA

FIRST INSTAR (Pl. 78, B, C).—The newly hatched larva is translucent whitish in color; the average length of three larvæ was 0.4208 mm. and the greatest width 0.1315 mm. The larva tapers toward each extremity, the greatest diameter being about the third thoracic segment; the larva is pointed posteriorly. Just before the first molt is cast the head is much narrower than any of the first 8 body segments. On the front of the head are two rather long fleshy protuberances which very probably are the antennæ. The antennæ in this instar are fully as long as in any of the succeeding instars, if not longer. There are four pairs of rather prominent setæ on the head, one pair just above and inside the antennal area, two pairs above the mandibles, and a pair laterad of the antennæ. The mandibles (Pl. 76, N) in this stage are simple hooks which are very highly chitinized and very slender and pointed. The whole head shield is more highly chitinized than in later instars. The body is composed of the usual 13 segments which bear 5 pairs of spiracles, a pair to each of the last 2 thoracic and first 3 abdominal segments. There are two rows of subdorsal setæ the full length of the body that are extremely prominent, giving the larva almost the appearance of an Indian war bonnet when seen in profile (Pl. 78, B, C). There are 2 lateral rows in which the setæ on the first 2 thoracic segments are exceedingly prominent, being nearly three times the length of any of the remaining setæ in these rows. There are also 2 subventral rows on the thoracic segments only. In addition to the setæ just described, each segment is rather densely covered with very minute setæ which are not present in the succeeding instars.

SECOND INSTAR (Pl. 78, D).—The color and general shape are the same as in the previous instar, except that the abdomen is not so pointed. The head of the larva is much blunter anteriorly than in the previous instar. Three larvæ in this instar averaged 1.050 mm. in length and 0.4316 mm. in greatest width. The antennæ are slightly less prominent and the setæ very much less prominent than in the previous instar.

There are 5 pairs of small setæ on the head—a pair just above the mandibles, a pair laterad of these, a pair dorso-mesad of the antennæ, a pair caudo-dorsad of the antennæ, and a pair on top of the head. The mandibles (Pl. 76, O) have changed shape considerably and are now much broader at the base and are less slender and less chitinized than in the previous instar. The labrum bears 4 heavily chitinized lobes or denticles. The body bears 9 pairs of spiracles, a pair being borne on each of the last 2 thoracic and first 7 abdominal segments. The setæ on the body in this instar are very small and inconspicuous. There are 2 subdorsal rows, 2 lateral or spiracular rows, and 4 subventral rows on the thoracic segments; also 4 additional subdorsal setæ on the first thoracic segment and 2 subventral setæ on both the eighth and ninth abdominal segments.

THIRD INSTAR (Pl. 78, E).—The color and general shape are very much as in the previous instar. Four larvæ in this instar averaged 1.610 mm. in length and 0.4925 mm. in greatest width. The setæ on the head are slightly more prominent. There are 5 pairs of setæ located as in previous instar. Antennæ as in previous instar. Mandibles (Pl. 76, P) with general shape same as in previous instar, although they have increased considerably in size. The labrum in this instar has 4 prominent chitinized denticles or lobes and a rather inconspicuous one at each side of these. Spiracles as in previous instar. Between the last 2 thoracic, the last thoracic and first abdominal, first and second, and second and third abdominal segments there are rather prominent, fleshy, dorsal folds. The setæ are slightly more prominent and are arranged as in previous instar, except for 1 additional subventral pair on first thoracic segment, and an additional pair of spiracular setæ on the sixth and seventh abdominal segments.

FOURTH INSTAR (Pl. 78, F).—Color, general shape, head, antennæ, and setæ of head as in previous instar, except that the setæ are much more conspicuous. Two larvæ in this instar averaged 1.855 mm. in length and 0.6300 mm. in greatest width. The mandibles (Pl. 76, Q) in this instar are stouter and more heavily chitinized than in the previous instar. There are 4 heavily chitinized lobes to the labrum with an inconspicuous lobe on each side of them. Spiracles as in previous instar. The dorsal fleshy folds same as in the previous instar with an additional one between the third and fourth abdominal segments. This character is probably somewhat dependent upon the position the larva is in at the time of observation. The body setæ are slightly more prominent than in the previous instar. There are 14 setæ on the first thoracic segment, 8 on both the second and third thoracic segments; 4 setæ on each of the first 5 abdominal segments, 6 on each of the sixth, seventh, eighth, and ninth abdominal segments, 4 on the tenth. The setæ are arranged as shown in Plate 78, F.

The full-grown larva (Pl. 76, U; fig. 16) is less translucent and the color is more grayish white than in the previous instar. There is a darker area almost the full length of the larva due to the contents of the digestive tract. The general shape of the larva is the same as in the previous instar. There is a distinct lateral invagination of the last abdominal segment. The dorsal folds are more prominent than in the previous instar, and there are usually more of them. The setæ are more prominent than in any previous instar except the first. Four full-grown larvæ averaged 2.485 mm. in length and 0.735 mm. in greatest width. Head as in previous instar. Mandibles (Pl. 76, R) very stout and heavily chitinized. The labrum (Pl. 76, S) is a large, rectangular, fleshy piece that almost covers the mandibles. On the inner surface near the distal margin are from 5 to 7 prominent denticles or lobes which are apparently very heavily chitinized; the labrum also bears 2 minute setæ. The maxillæ and labium (Pl. 76, T) are fused and only very slightly chitinized on the surface; they bear 6 minute setæ and in addition 2 groups of slight

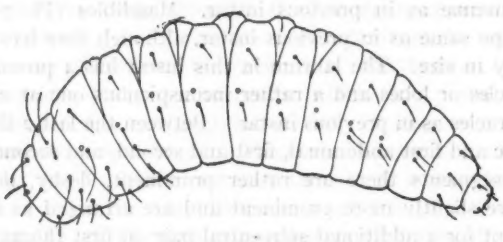


FIG. 16.—*Eupelmus allynii;* Lateral view of full-grown larva. × 30.6.

elevations or tubercles containing 3 elevations each, 2 groups containing 2 each, and 4 single scars or elevations. All are arranged as in Plate 76, T. Spiracles as in previous instar. Setæ as follows: 14 on the first thoracic, 10 on each of the second and third thoracic segments, 4 on each of the first 5 abdominal, 6 on each of the last 5 abdominal segments. Setæ arranged as shown in figure 16.

The number of larval instars and molts were ascertained in the manner described for *Ditropinotus aureoviridis*, page 411–412. There were found to be 4 larval molts with 5 pairs of larval mandibles (Pl. 76, N–R) as for *D. aureoviridis*. The manner of feeding and locomotion is also similar to that of *D. aureoviridis*. Thirty-two larvæ reared in glass cells in 1918 became full-grown in from 7 to 12 days, depending upon weather conditions. The average length of this period was 9 days, or an average of about 2.25 days per molt. Twenty-seven of these larvæ were inactive for from 2 to 17 days, an average of 5 days, before beginning pupation. In 1917, 28 individuals averaged 16 days in the larval stage from egg to prepupa.

This species proved to be much more tractable than either of the other two treated in this paper. They bred freely in the cell slides through five generations during the breeding season of 1918. The larvæ are very active and are voracious feeders. Never more than one individual was found to develop upon a single host larva, though as many as 8 eggs have been found in a single jointworm cell that was taken from a breeding cage. Under field conditions, however, this would scarcely obtain, since the jointworm cells so far outnumber the adults of *Eupelmus allynii* which are present.

PREPUPA

The prepupal stage (Pl. 78, G; 77, G) for 17 individuals of this species ran from 1 to 3 days, the average being 1.7 days. Upon entering this stage the larva voids considerable excrement, the prepupa being then pure white in color. At no other time has the larva ever been observed to void excrement. Upon entering this stage the larva contracts both in length and width. The third thoracic and first, second, and third abdominal segments become much shorter. There are numerous lateral fleshy folds at this time. The setæ are arranged the same as are those of the full-grown larva.

PUPA

When the pupa (Pl. 77, H) is first formed it is pure white. It gradually changes to intense black. Larvæ of this species that became full-grown in glass cells late in the fall usually did not pupate until the following spring, although a few remained in the pupal stage through the winter when kept in a cold cellar. Sixty-two individuals remained in the pupal stage from 7 to 33 days during the breeding season, depending upon weather conditions. The average length of the pupal period was 21 days. The pupa of the male is smaller than that of the female; the average length of 5 male pupæ was 2.142 mm. and the greatest width was 0.658 mm. The average length of 4 female pupæ was 3.0275 mm., and width 0.7875 mm.

ADULT

This species (fig. 13; 14; 15, *a*, *b*) overwinters as full-grown larvæ in the jointworm cells in old wheat stubble, the first adults emerging the latter part of April or the first week in May, in Virginia. Males normally occur, though under cage conditions this species will reproduce parthenogenetically, unfertilized females producing male progeny only.

The adults of this species are very active, and soon after emergence the females run rapidly up and down the old wheat stubbles nervously stroking the stubble with their antennæ in a diligent search for a suitable place to oviposit. They fly very quickly and rapidly but apparently only a few feet at a time. The manner of oviposition is

practically the same as that of *Ditropinotus aureoviridis* (see p. 414–415). The process of oviposition usually requires several minutes. One female *Eupelmus allynii* lived 52 days and oviposited over a period of 32 days. Four generations were reared in glass cell slides during the breeding season of 1918, starting with females that emerged from material collected the previous fall and kept under as nearly normal conditions as possible.

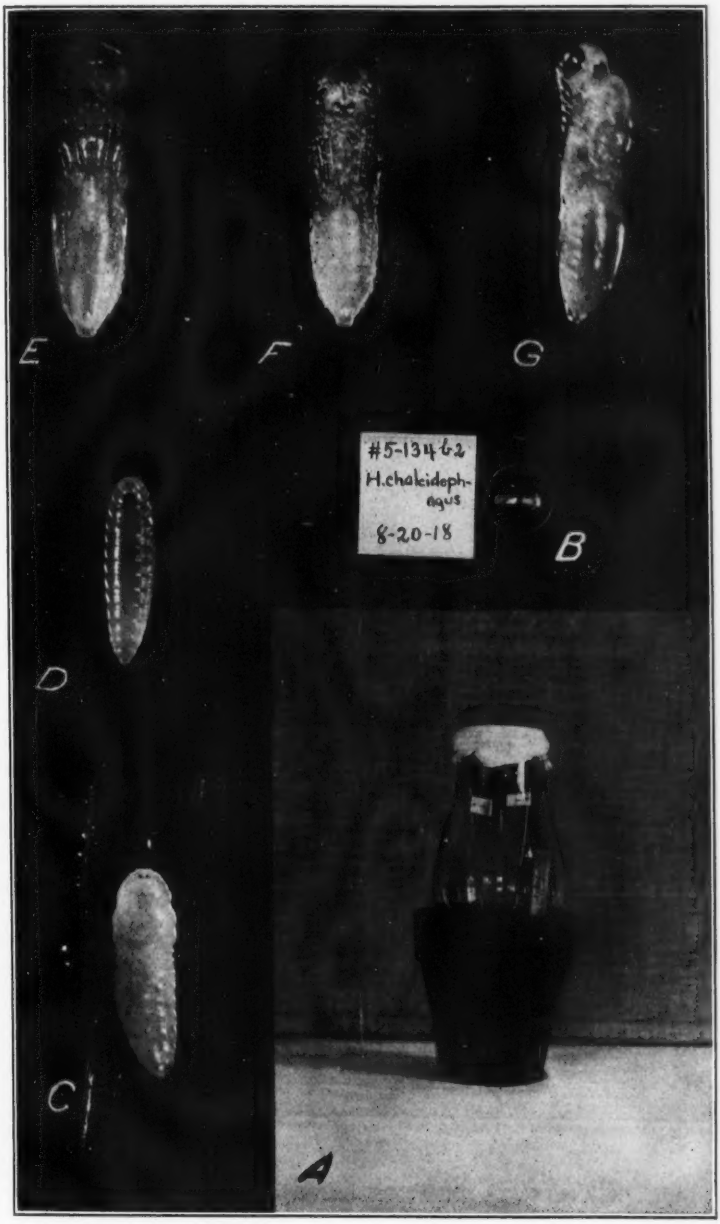
CONCLUSIONS

Judging from the observations recorded herewith and from the field observations of the season of 1919, it is quite clear why the parasites do not quickly gain complete control of the wheat jointworm. The writers have found that as the parasites become more abundant hyperparasitism increases greatly. Some of the parasites that are primary only, when present in small numbers, become both primary and secondary as they become more abundant.

At the close of the season in 1919 at Warrenton, Va., *Homoporus chalcidiphagus*, a purely primary parasite, was very scarce indeed, while in 1916 it was one of the most important. This condition is undoubtedly due to other parasites existing upon it as secondaries. *Eurytoma* sp. was the most important parasite present at Warrenton in the fall of 1919 and *Ditropinotus aureoviridis* and *Eupelmus allynii* were turning their attention largely to this species, since *Harmolita tritici* was greatly in the minority. While *Harmolita tritici* has been greatly in the minority in the fall in proportion to the number of its parasites present, for several years at Warrenton, the percentage of jointworm-infested wheat plants has remained about constant from year to year. This is further evidence that hyperparasitism has been going on continuously. Therefore it would seem that the parasites can be relied upon for only partial and not complete control.

PLATE 74

A.—Lantern globe breeding cage.
B.—Glass cell slide observation cage.
C.—Ventral view of the prepupa of *Homoporus chalcidiphagus*. × 13.
D.—Ventral view of full-grown larva of *H. chalcidiphagus*. × 9.4.
E.—Ventral view of female pupa of *H. chalcidiphagus*. × 12.9.
F.—Ventral view of male pupa of *H. chalcidiphagus*. × 14.5.
G.—Lateral view of pupa of *H. chalcidiphagus*. × 12.9.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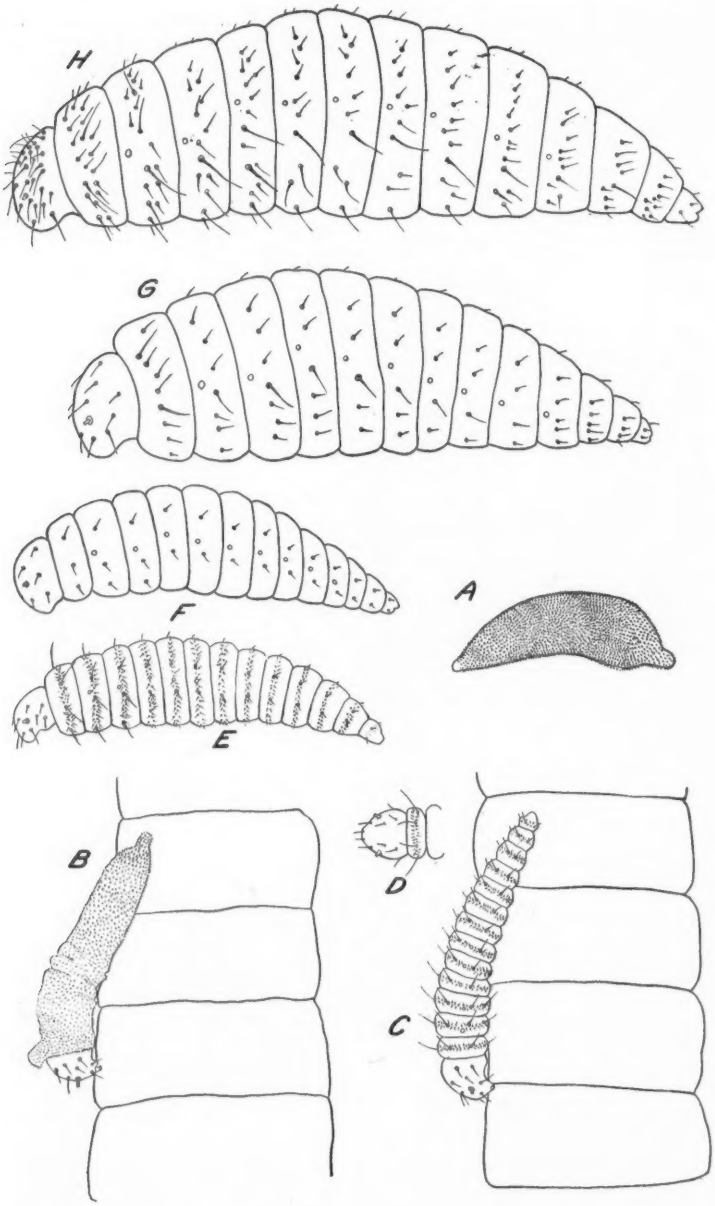
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PLATE 75

A.—Egg of *Ditropinotus aureoviridis*.

B.—Lateral view of *D. aureoviridis* larva hatching.

C.—Lateral view of *D. aureoviridis* larva just after hatching. Note the comparative size of larva and host.

D.—Dorsal view of head of first-instar larva of *D. aureoviridis*.

E.—Lateral view of first-instar larva of *D. aureoviridis* just before casting first molt.

F.—Lateral view of second-instar larva of *D. aureoviridis*.

G.—Lateral view of third-instar larva of *D. aureoviridis*.

H.—Lateral view of fourth-instar larva of *D. aureoviridis*.

All greatly enlarged.

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PLATE 76

A.—Mandibles of first-instar larva of *Ditropinotus aureoviridis*.
B.—Mandibles of second-instar larva of *D. aureoviridis*.
C.—Mandibles of third-instar larva of *D. aureoviridis*.
D.—Mandibles of fourth-instar larva of *D. aureoviridis*.
E.—Mandibles of full-grown larva of *D. aureoviridis*.
F.—Mouthparts of full-grown larva of *D. aureoviridis*.
G.—First-instar mandibles of *Homoporus chalcidiphagus*.
H.—Second-instar mandibles of *H. chalcidiphagus*.
I.—Third-instar mandibles of *H. chalcidiphagus*.
J.—Fourth-instar mandibles of *H. chalcidiphagus*.
K.—Mandibles of full-grown larva of *H. chalcidiphagus*.
L.—Mouthparts of full-grown larva of *H. chalcidiphagus*.
M.—Ventral view of head of full-grown larva of *H. chalcidiphagus*.
N.—Mandibles of first-instar larva of *Eupelmus allynii*.
O.—Mandibles of second-instar larva of *E. allynii*.
P.—Mandibles of third-instar larva of *E. allynii*.
Q.—Mandibles of fourth-instar larva of *E. allynii*.
R.—Mandibles of full-grown larva of *E. allynii*.
S.—Labrum of full-grown larva of *E. allynii*.
T.—Mouthparts of full-grown larva of *E. allynii*.
U.—Lateral view of head of full-grown larva of *E. allynii*.
All greatly enlarged.

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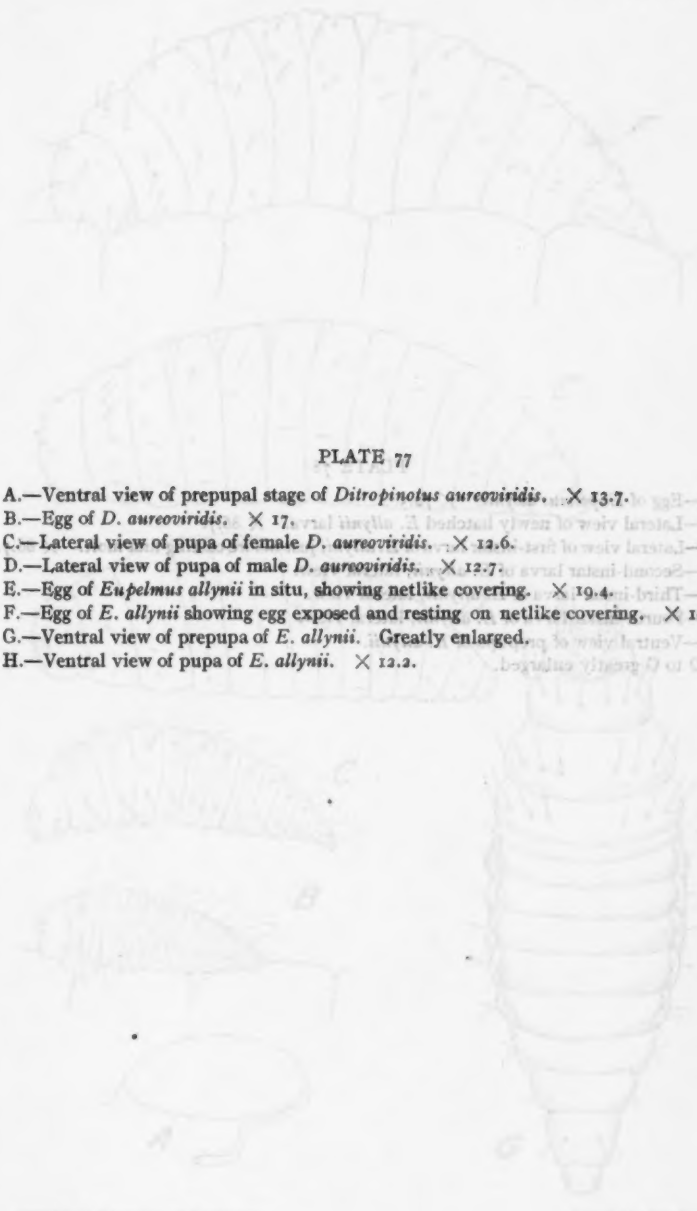
PLATE 77

A.—Ventral view of prepupal stage of *Ditropinotus aureoviridis*. × 13.7.
B.—Egg of *D. aureoviridis*. × 17.
C.—Lateral view of pupa of female *D. aureoviridis*. × 12.6.
D.—Lateral view of pupa of male *D. aureoviridis*. × 12.7.
E.—Egg of *Eupelmus allynii* in situ, showing netlike covering. × 19.4.
F.—Egg of *E. allynii* showing egg exposed and resting on netlike covering. × 19.4.
G.—Ventral view of prepupa of *E. allynii*. Greatly enlarged.
H.—Ventral view of pupa of *E. allynii*. × 12.2.



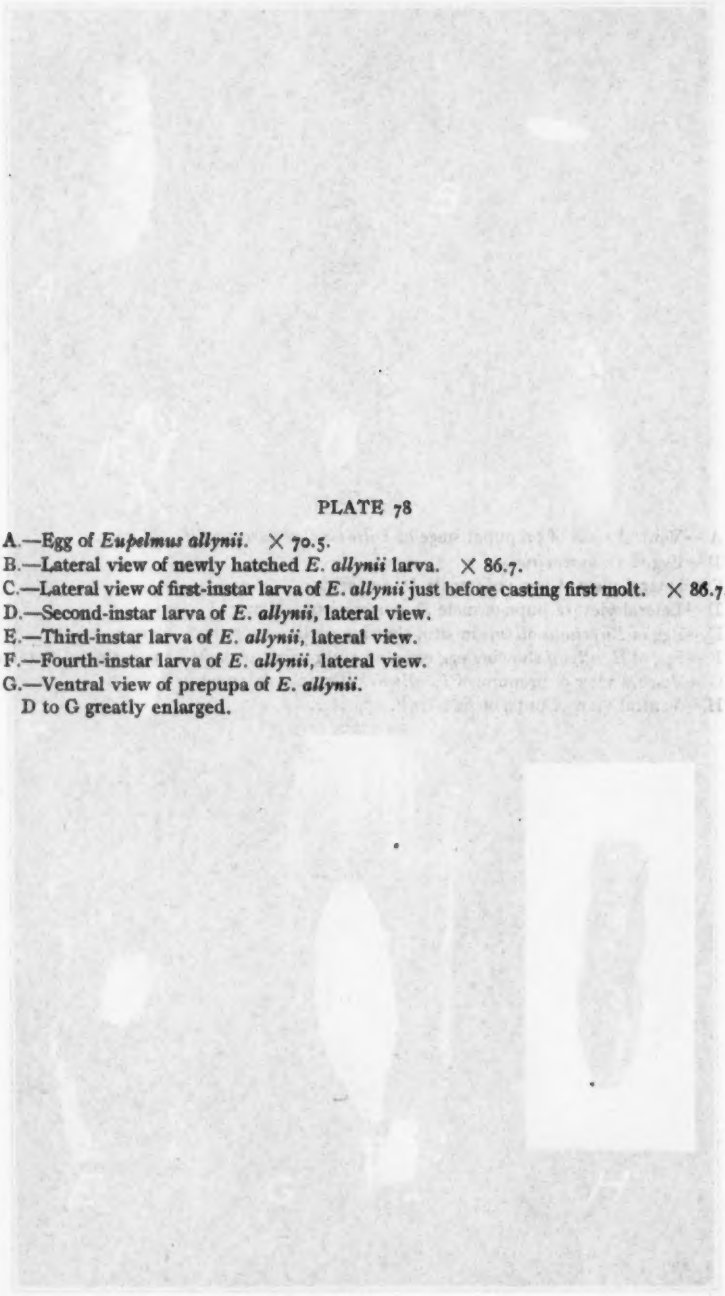
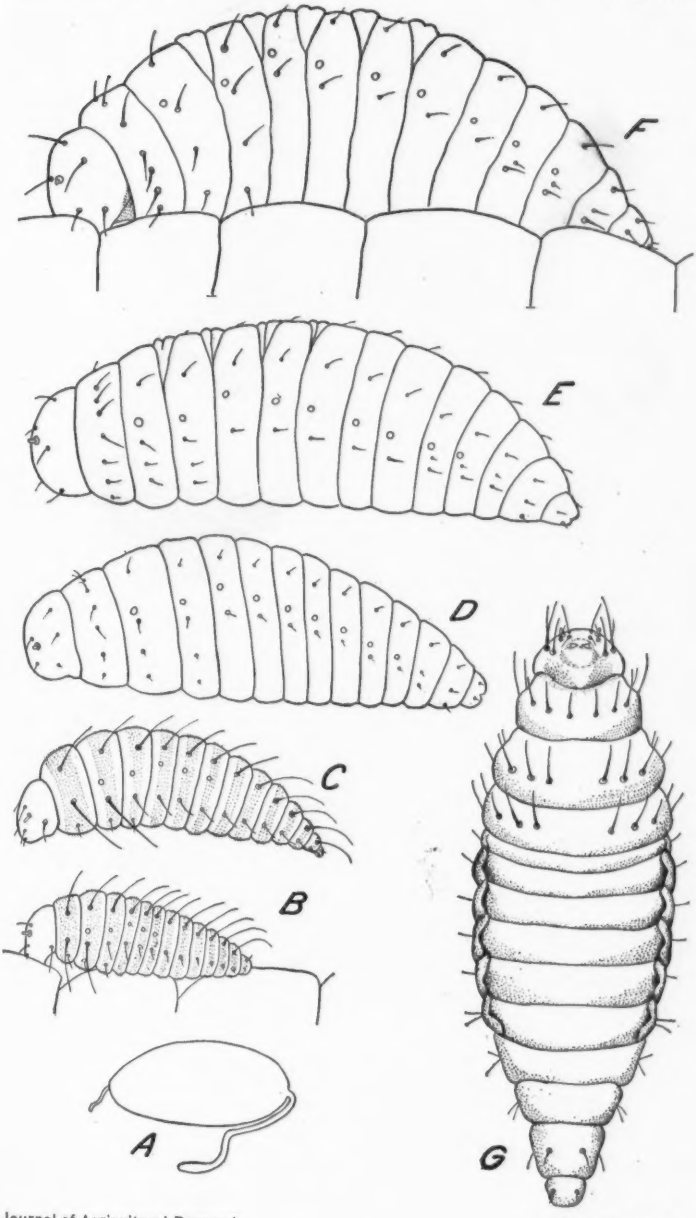


PLATE 78

A.—Egg of *Eupelmus allynii*. × 70.5.
B.—Lateral view of newly hatched *E. allynii* larva. × 86.7.
C.—Lateral view of first-instar larva of *E. allynii* just before casting first molt. × 86.7.
D.—Second-instar larva of *E. allynii*, lateral view.
E.—Third-instar larva of *E. allynii*, lateral view.
F.—Fourth-instar larva of *E. allynii*, lateral view.
G.—Ventral view of prepupa of *E. allynii*.
D to G greatly enlarged.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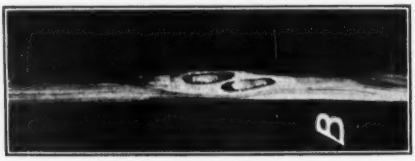
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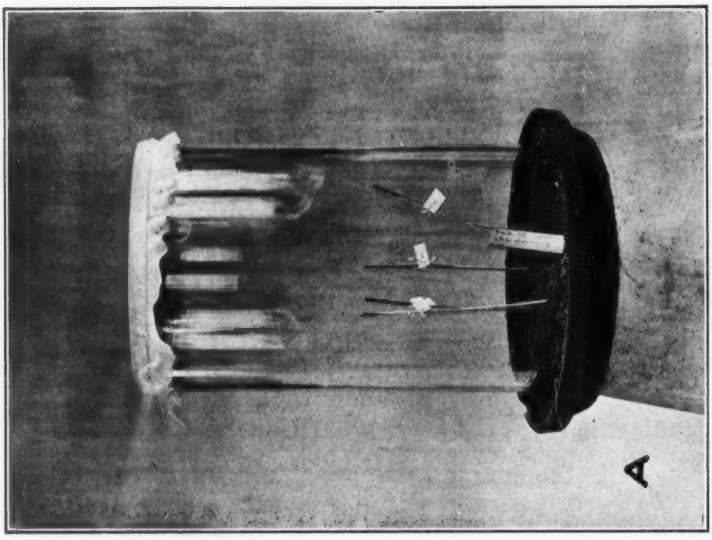
A

PLATE 79

A.—Glass cylinder breeding cage, 9 by 14 inches.

B.—Two individual cells of a gall caused by the wheat jointworm in the culm, or stem, of the wheat.